Comparative nutrition and energy metabolism of young red deer (*Cervus elaphus*) and red x elk hybrid deer.

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To those who have influenced my genes
and my environment

Abstract of a thesis submitted
in partial fulfilment of the requirements for
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H.G Judson

Elk (*Cervus elaphus spp*) are widely used as a terminal sire in the New Zealand deer industry because elk red deer crosses are heavier at 12 months of age than pure-bred red deer (*Cervus elaphus*) and therefore better fit market demands. However, it is unclear whether nutritional requirements differ between genotypes. A series of experiments compared young (4 - 12 months) red deer and red deer - elk cross (hybrids) in various aspects of their nutrition.

Single genotype groups (10-15) of red deer and hybrid weaner stags were offered one of four pasture allowances (2 to 12 kg DM/head/day) on a rotationally grazed mixed ryegrass – white clover pasture system for 9 weeks in winter (June-July), spring (October-December) and summer (February - March). Stags were weighed and given a new allocation of pasture weekly. Pre-grazing pasture mass ranged from 800 kg DM/ha for low pasture allowances to 4500kg DM/ha for higher allowances. Winter liveweight gain was low (40-80 g/day), relatively unaffected by pasture allowance and similar for both genotypes. In spring however, hybrids gained liveweight on average 100 g/day more than red deer across all pasture allowances and the response to additional pasture allowance was large (110 g/day at 2kg DM/head/day to 300 g/day at 9.5 kg DM/head/day). At the highest pasture allowance, hybrids grew faster (350 g/day) than red deer (250 g/day), although red deer were able to achieve this liveweight gain when offered less pasture (4 vs 12 kg DM/head/day, respectively). Summer liveweight gain was lower for both genotypes and responded less to increases in pasture allowance than during spring.

A second experiment compared the liveweight gain of both genotypes at *ad lib* feeding in an indoor environment where intake could be accurately measured.
A group of red deer (n =15) and a group of hybrid (n =15) weaner stags were housed indoors during winter (3 June - 27 August) and spring (16 October - 16 December) and fed a pelleted grain based ration *ad lib*. Mean daily intake for each group (kg DM/head/day) was calculated as the difference between feed offered and feed refused.
Hybrids had a significantly higher ($P< 0.05$) absolute DM intake compared with red deer in both seasons, although when expressed on a metabolic body weight basis, there was no difference between genotypes irrespective of season. Liveweight gain during winter did not differ significantly between genotypes regardless of whether it was expressed on an absolute or metabolic weight basis. Spring

liveweight gain, expressed both on an absolute and metabolic liveweight basis, was significantly higher for hybrids compared with red deer ($P<0.05$).
Red deer and hybrids increased their feed intake from winter to spring by 20% and 24% respectively on a metabolic body weight basis. Although the difference between genotypes in their seasonal increase in intake was relatively small there was a large difference in their pattern of liveweight gain. Red deer exhibited a 34% and hybrids a 76% seasonal increase in liveweight gain expressed on a metabolic liveweight basis from winter to spring.
These results indicate the greater rate of liveweight gain displayed by hybrids compared with red deer was not associated with a greater *ad lib.* intake (expressed on a metabolic body weight basis) and the seasonal increase in liveweight gain is greater for hybrids than for red deer.

A further experiment estimated the energy requirement for maintenance of both genotypes.
Five deer of each genotype were housed in separate pens ($3.5m^2$) during winter (3 June - 27 August) and spring (16 October - 16 December) and randomly assigned to one of 5 feeding levels (0.5, 0.6, 0.7, 0.8, or 0.9 times estimated *ad lib.* intake of 1.5 and 1.7 kg DM/head/day during the winter and 3.0 and 3.3 kg DM/head/day during the spring for red deer and hybrids, respectively. Maintenance requirement was determined by regression analysis of liveweight gain on ME intake.
Although there was no seasonal effect on the liveweight gain response to intake there was a significant genotype effect. To maintain liveweight during either season, hybrids required a higher ME intake (0.52 MJ ME/$W^{0.75}$/day compared with red deer 0.41 MJ ME/$W^{0.75}$/day). The rate of increase in liveweight gain to increasing intake declined as intake increased and more so for red deer than hybrids.

The final experiment in the series involved individually housed deer and aimed to more precisely determine differences in maintenance requirement and examine the difference in composition of gain between genotypes. In addition, *in vivo* apparent DM digestibility was measured in both genotypes.

Red deer (n=7) and hybrid weaner stags (n=7) were housed in individual pens for a period of 8 weeks in both winter (July - August) and spring (November - December) and offered one of 7 feeding levels which ranged from maintenance to *ad lib.* During each 8 week experimental period, liveweight gain, apparent digestibility and feed intake were measured. Immediately prior to, and at the conclusion of each 8 week period body composition was estimated using computer-assisted topography (CT scan).

In winter, there was no significant difference in the liveweight gain response to intake although red deer tended to have a higher (44 vs 55 MJ/kg) requirement for gain than hybrids. In spring, red deer had a lower requirement for maintenance (0.35 vs 0.47 MJ ME/$W^{0.75}$/day) but a greater requirement for liveweight gain (64 vs 35 MJ/kg) than hybrids. In spring, mean *ad lib.* intake was about 30%

higher than in winter and was greater for hybrids than for red deer. Energy retention in whole body (kJ/W $^{0.75}$/day) did not differ between genotypes in either winter or spring but both the energy requirement for zero energy balance (0.59 vs 0.48 MJ ME/W $^{0.75}$/day) and the efficiency of utilisation (0.37 vs 0.24) was greater in spring than in winter. The disparity between liveweight gain and whole body weight gain may have been due to differences in gut fill.

There was no significant difference between genotypes in relative growth coefficients for lean, bone or adipose tissue in whole body. However hybrids tended to have a higher winter and lower spring growth coefficient for fat compared with red deer. Growth coefficients for adipose, lean and bone, respectively were 0.983, 1.063 and 1.026 for winter and 1.02, 0.708 and 1.727 for spring. At the same whole body weight, deer in October had less adipose tissue than in August. It is unclear whether this represents a strategy for rapid spring growth or is an artefact of experimental protocol.

Apparent dry matter digestibility (DMD) did not differ between genotypes but was higher by between 7 and 15 percentage units in winter compared with spring. Unexpectedly, digestibility was positively correlated with intake. Digestibility increased by 2.6 percentage units for every 10g DM/W$^{0.75}$/day increase in either season in one group and 4.1 and 2.1 percentage units for deer in winter and spring respectively in another group. Errors in faecal collection were discounted as causes of the unexpected result

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Chapter 1

Introduction

Deer production has increased in significance to the New Zealand animal industry over recent years and currently export returns from the deer industry exceed $213 M of which $157 M comes from venison (Statistics New Zealand, 1999).

Integrated livestock production systems often involve the use of terminal sires to produce animals specifically for slaughter. Elk *(Cervus elaphus spp)* are becoming more widely used as terminal sires within the New Zealand deer industry because elk x red crosses (hybrids) have a higher weaning weight and faster pre- and post-weaning growth rate compared to red deer (Moore & Littlejohn, 1989). This advantage in growth rate enables producers to more easily attain the industry target slaughter weight (95 kg liveweight) within 12 months of age which coincides with the elevation in the venison schedule as a result of increasing Northern Hemisphere demand at this time.

It has been suggested that the liveweight gain advantage normally exhibited by red x elk hybrids over red deer is dependent on the level of feeding and in some situations where feed is limited the advantage to the hybrid may be much reduced or may not exist. While farm based observations suggest the liveweight gain difference between the genotypes is greater when large amounts of feed are offered and much smaller when feed is restricted, no formal comparisons of the two genotypes over a range of feeding levels has been reported.

The volume of New Zealand research on the nutrition of deer is modest and generally confined to red deer. This is a reflection of the fact that deer have only been farmed in New Zealand over the last 25 years. Research from Europe and North America has tended to study the nutrition of wild deer for wildlife management purposes rather than within a production system. As a consequence there are few formal investigations into the nutritional requirements of young red deer in a pastoral production system and even less work relating to farmed elk.

With elk type animals becoming more widely used as terminal sires and consequently "hybrids" becoming an increasing proportion of yearling deer slaughtered, information on the relative feed requirements is becoming increasingly important if efficient production of venison is to be achieved. Given the seasonal and geographic variation in pasture supply experienced in New Zealand it is

important as part of any evaluation of the potential use of elk in the deer industry that the extent to which genotypes differ in their nutritional requirements be investigated.

The aim of this study was initially to identify, in a series of formal scientific experiments, whether on-farm observations that red deer and hybrids differed in their production response to level of nutrition within a pastoral system. The basis for such differences were further investigated in controlled indoor feeding conditions and in body composition studies.

Chapter 2

Review of the Literature

2.0 Introduction

Elk are larger than red deer (Moore and Littlejohn, 1989) and therefore the former will grow more rapidly. This difference in mature body size is reflected in red x elk hybrid (hybrid deer) weaner stags increasing liveweight at a greater rate in the 12 month period post-weaning and being heavier at 12 months of age compared with red deer (Drew and Hogg, 1990; Walker *et al.,* 2000). Differences in liveweight gain at similar times of the year have typically ranged from 50 to 150 g/day. This variation is likely to reflect the proportion of elk genes present in the hybrid, nutritional environment and management.

Terminology

There is currently no consensus on the taxonomic classification of red deer and elk. Some classify red deer (*Cervus elaphus*) and elk (*Cervus canadensis*) as different species (Whitehead, 1972) while others (Tate *et al.,*1992; Fennessy and Pearse, 1990) believe them to be of the same species (*Cervus elaphus*) but red deer (*Cervus elaphus scoticus*) a different sub-species to elk (*Cervus elaphus nelsoni, Cervus elaphus roosevetii, Cervus elaphus manitobensis*).

A true hybrid is the result of a first cross between two different species. While it is acknowledged that the animals referred to as hybrids in this thesis do not fit the description of a hybrid because there is some debate whether the parents are truly different species and in addition they may not necessarily be the result of a first cross, the term hybrid has been used to describe elk/red x red offspring in line with similar research (Kusmartono *et al.,* 1995) and with current industry terminology.
In this thesis, red and hybrid deer are described as different genotypes. A genotype describes a group of animals with a common genetic composition at a specific gene locus or set of loci. While this term is normally reserved for selections within a breed (for example, Ball *et al.,* 1995; Smith *et al.,* 1997) it can equally apply to groups (cross-breeds) from more diverse genetic background (Nicoll *et al.,*1998) and can therefore be appropriate here.

Comparison between breeds and strains

Good scientific comparisons between breeds and/or strains of animals are difficult for a number of reasons.

1) the sample of the breed, strain, or genotype must fairly represent the within breed or strain diversity and
2) if crossbreds are involved in the comparison, the potential contribution of non-additive genetic effects such as heterosis must be acknowledged.

Good experimental design can ensure that groups are formed from a range of sources to cover the range of within breed variation although this will be more difficult in a newly domesticated species such as deer where genetic and phenotypic variation for productive traits is large (McManus, 1993).

The contribution of heterosis to the productivity of crossbred animals can be established by full reciprocal crossing experiments (for example, Baker *et al.*, 1986) but these demand large resources and these data currently do not exist for red elk hybrids. Failing these data for deer, extrapolation can only be made crudely from comparisons of the published performance of pure-bred and cross bred animals albeit in different environments. Mature liveweight is about 280 kg and 400 kg for red deer and elk males, respectively (Pearse, 1988). Yearling elk (12 months) are typically 155 kg (Wairimu *et al.*, 1982) while red deer at the same age weigh approximately 90-100 kg.

Much of New Zealand's early venison production is based on, not a first cross hybrid, but an animal that contains approximately 25% elk genes. Data from previous experiments with hybrids containing a similar proportion of elk genes (Kusmartono *et al.*, 1995) suggest best estimates of 12 month liveweight for red stags is 93 kg and for hybrids is 115 kg (Figure 2.1).

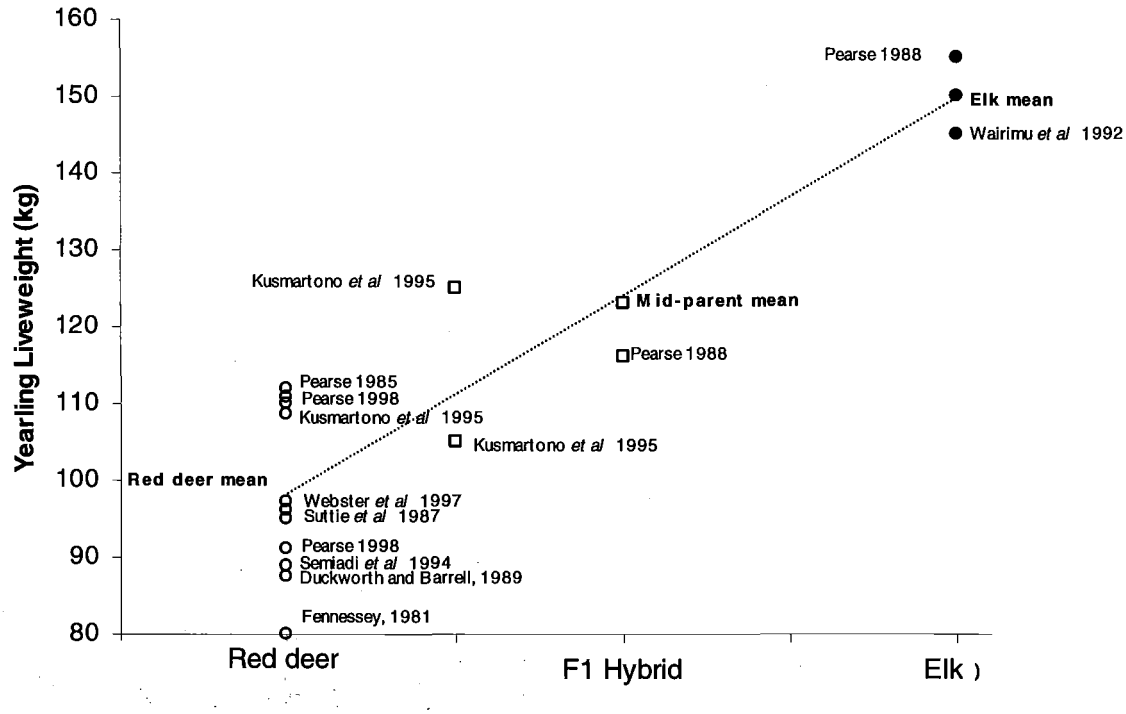


Figure 2.1. *Previous published values of 12 - 15 month liveweight (kg) for red deer (O), elk (●) and their hybrids (□).*

The previous published value for 12 month weight of 25:75 red-elk hybrid deer (123 kg) suggests they are heavier (13.5 kg) than would be expected based on previously published values of 12 month weigh of the pure bred parents (96 and 150 kg for red deer and elk, respectively). This corresponds to a 12% heterosis figure for liveweight in hybrid deer. However, estimates of heterosis based on these data are crude, given parental means represent many different environments.

Superior liveweight gain of hybrid deer has been demonstrated in both a research environment (Pearse, 1988) and on farm (Walker *et al.*, 2000; Beatson *et al.,* 2000) but the mechanisms by which hybrids are able to achieve a higher liveweight gain are not clear. Identifying the mechanisms involved would help producers more consistently achieve high liveweight gain. For example, greater liveweight gain is usually associated with a greater feed intake (Semiadi, *et al.,* 1993a) but a lower stocking rate (higher pasture allowance). However, other possible mechanisms may also be responsible for greater liveweight gain (Figure 2.2).

Greater liveweight gain at a common relative intake would be expected if animal exhibited;

(1) a higher digestibility of gross energy consumed
(2) a higher metabolisability of digestible energy
(3) a lower maintenance requirement and therefore more energy for production
(4) a higher efficiency of utilisation of ME for fat and/or protein deposition
(5) a higher protein : energy ratio (protein : fat) in liveweight gain

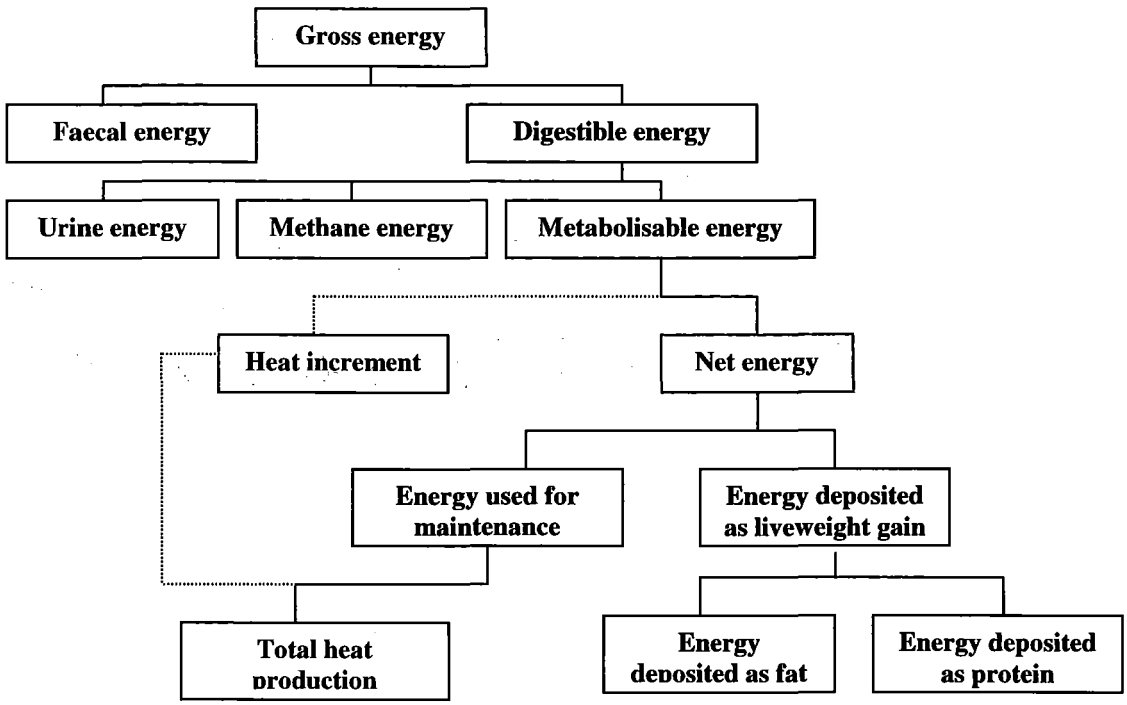


Figure 2.2 *Partitioning of gross energy in the animal. Shaded boxes represent mechanisms which at a common intake could be expected to support a greater liveweight gain.*

The aim of this section is to review the factors affecting grazing intake and partitioning of gross energy and establish whether there is evidence for difference between genotypes.

2.1 Intake

Introduction

Pasture intake is the single most important factor affecting production levels of grazing ruminants (Poppi *et al.*, 1987; Rattray and Clark, 1984). The amount of feed consumed by grazing ruminants has been estimated by Ulyatt (1984) to account for 50 to70% of the variation between pastures in their capacity to sustain animal productivity. There are three main factors controlling feed intake. Firstly, intake is proportional to nutrient demands. For example, lactating females have a higher *ad lib.* intake than non-lactating cohorts (Poppi *et al.*, 1987). Differences in energy demands between red deer and hybrids may lead to a difference in intake and are discussed in a later section (Section 2.2). Secondly, pasture intake is dependant on the rate of clearance of digesta from gastrointestinal tract. Digesta clearance from the rumen is a major factor determining *ad lib* feed intake (Black *et al.*, 1982).

Finally, pasture intake is dependant on pasture availability and in particular pasture allowance. Of the variables which influence nutrient concentration, digestibility and metabolisability of the diet may vary by a factor of 2 and 1.2 respectively, whereas herbage intake may vary by a factor of 5 depending on sward conditions (Hodgson and Grant, 1981; Minson, 1982). Therefore, the major factor influencing pasture intake is likely to be pasture allocation rather than nutritional factors or animal demand.

Nutrient Demand

Grazing intake is proportional to the nutrient demand of the animal and therefore intake is generally higher for large and high producing breeds. For example, L'Huillier *et al.* (1988) reported Friesian cows (418 kg) grazed to a lower post-grazing pasture height (3.4 cm vs 3.7 cm) than Jersey cows (342 kg) when offered similar pasture allowances (per cow per day) of the same pre-grazing height and therefore had a greater apparent DM intake. Furthermore, high breeding value (BV) Friesian dairy cows (126 breeding indices) are known to have a higher ME intake (2.07 MJ ME/W $^{0.75}$/day) in stall feeding situations fed pasture compared with their low BV (102 breeding indices) counterparts (1.99 MJ ME/W $^{0.75}$/day) (Davey *et al.*, 1983). Similar work with Jersey cows in a pastoral environment (Bryant, 1983), showed high BV cows consumed a greater proportion of herbage offered (65.3%) than low BV cows (61.0%).

It is probable, hybrid deer, with their greater potential for liveweight gain, have a greater nutrient demand compared with red deer. However, the difference in liveweight (10-15 kg) between genotypes as young weaner stags is not large and unless there is big differences in the composition of gain differences in nutrient demand are likely to be small.

Rumen disappearance rate

Pasture intake can be dependant on the rate of disappearance of digesta from the rumen (Black *et al.*, 1982). Disappearance rate is a function of the degradation rate of material consumed and passage or outflow rate of digesta.

The outflow of particles from the rumen primarily depends of the rate of breakdown of particles to sizes which have a high probability of passage from the rumen (Ulyatt *et al.*, 1986). For deer this has been defined as passage through a 1mm sieve (Domingue *et al.*, 1991a). Because soluble carbohydrates degrade about 150 times faster and storage carbohydrates about 5 times faster than structural carbohydrates (Maeng and Baldwin, 1976) the relative proportion of these constituents in plant material (a measure of quality) can affect the rate of removal from the rumen.

Generally, a slow passage rate through the gastrointestinal tract reduces intake while rapid passage rate increases intake. For example, a faster rumen clearance rate of chicory relative to ryegrass fed deer was associated with a higher *ad lib.* feed intake (Kusmartono *et al.*, 1997) and red deer fed red clover had a faster clearance rate and greater intake than on a ryegrass based pasture (Freudenberger *et al.*, 1994).

Both animal and feed factors affect rate of passage. Increased passage rate are generally associated with a higher DM intake (Warner, 1981) finely ground feeds which rapidly degrade to fine particles in the rumen (Blaxter *et al.*, 1956), feeds with low specific gravity (Campling and Freer, 1962) and feeds with a high fibre content (Warner, 1981). Animal factors include age, pregnancy, temperature and frequency of feeding with pre-ruminant (Warner, 1981), pregnant animals (Graham and Williams, 1962) in cool environments (Westra and Christopherson, 1976) have faster passage rates. In addition, a review of the literature suggests animals fed more frequently may have a faster passage rate compared to those which were given a single meal (Warner, 1981).

Pasture availability

Pasture availability to grazing livestock has been defined in a variety of terms such as pre- or post-grazing pasture mass, pasture allowance or pasture height. A pasture allowance is the amount of herbage existing above ground, offered to stock over a set period and is expressed in terms of kg DM/head/day or kg DM/100 kg/day. Pre- and post-grazing mass refer to the mass of herbage above ground per unit area before and after grazing respectively and are expressed as kg DM/ha. Where animals are stocked on areas continuously as opposed to a rotational system of stocking, pasture height is a more common definition of pasture availability.

Limited pasture allocation, irrespective of how it is defined, has a direct effect on pasture intake. Accurate measurement of grazing intake is difficult so many studies have used liveweight gain or other aspect of production (such as milk production) as a substitute for animal intake in defining relationships between animal intake and pasture availability.

The relationship between the amount of pasture allocated to the grazer, regardless of how it is defined, and pasture intake or it associated liveweight gain is curvilinear under most conditions (Figure 2.3). This relationship represents an increasing rate of decline in intake (or liveweight gain) with decreasing pasture allowance. Where pasture allowance is small (at the ascending part of the relationship) harvesting constraints are most important in limiting intake (and liveweight gain).

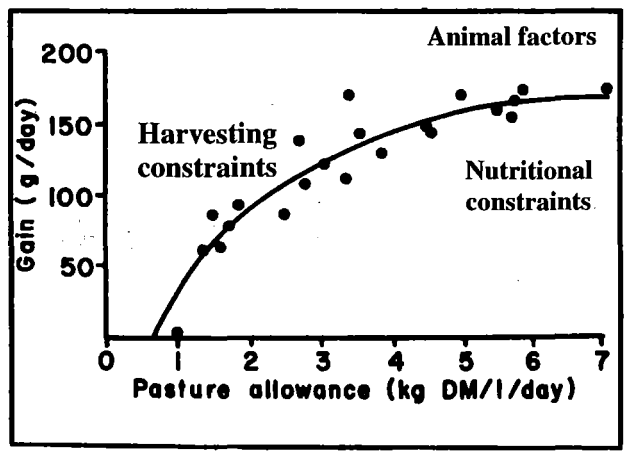


Figure 2.3. *A typical relationship between daily liveweight gain (g/day) of lambs and pasture allowance (kg DM/h/day) (from Rattray and Clark, 1984).*

Where pasture allowance is high and sward characteristics do not restrict the ability of animals to harvest pasture, nutritional factors such as animal nutrient demand, digestibility, rumen degradation rate and concentration of metabolic products, become important in controlling intake. Most farming systems generally operate over a range of pasture allowances corresponding to the steeper slope of the curve and therefore it is pasture variables which have the most pronounced influence on feed intake and animal production in these cases.

Grazing intake is a product of bite size, bite rate and grazing time. Daily herbage intake is closely correlated with bite weight since a low bite weight cannot be totally compensated for by increasing bite rate or grazing time (Hodgson, 1990). The major sward parameters which affect bite weight are pasture height and bulk density (Black and Kenney, 1984; Hughes *et al.*, 1991). Pasture height has little effect on bite area (area grazed by one bite) but taller pasture increased bite weight through a greater bite depth (the average length of removed leaves). For example, doubling sward height (within the range of 3 to 21 cm) increased bite weight of young red deer hinds, by 64% on average (Mitchell *et al.*, 1991). Breeding ewes in late pregnancy grazing a common allowance but at two

contrasting masses differed in both their intake and liveweight gain (Rattray *et al.*, 1982a). More extensive work (Rattray *et al.*, 1983) has produced a set of curves indicated the effect of increasing pasture mass on intake over a range of allowances (Figure 2.4).

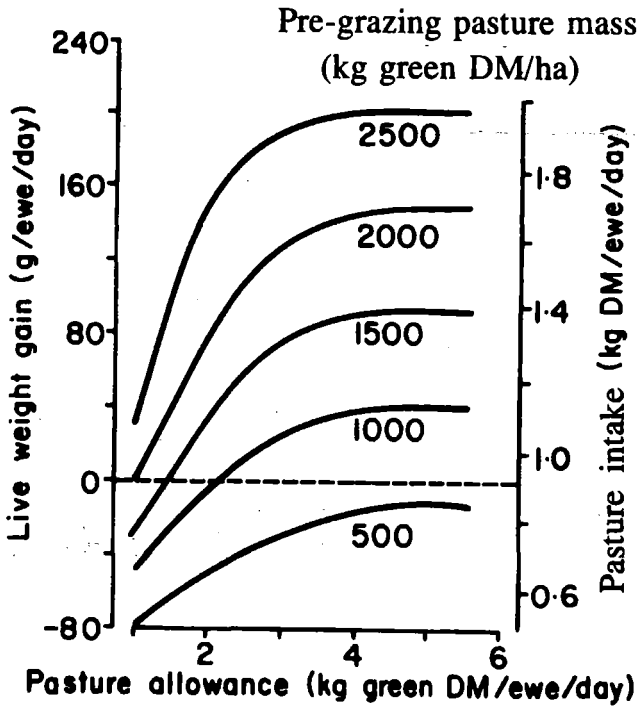


Figure 2.4. *The effect of pasture mass on intake and liveweight gain of ewes offered pasture at varying pasture allowances (from Rattray and Clark, 1984).*

Increasing pasture density also increases bite weight despite a reduction in both components of bite volume (bite area and bite depth). For example, doubling bulk density (within the range 0.19 - 0.75 mg DM/cm) increased bite weight by 21% (Mitchell *et al.*, 1991).
Increasing pasture height and density, increased bite weight and the effects of pasture height and density on bite weight are independent and additive (Hodgson, 1981). Pasture height has 3 times the effect on bite weight as pasture density. Therefore, it is pasture height rather than bulk density component of pasture mass that has the major effect on allowance - intake relationships.

There is a strong relationship between sward structure and animal performance. For example, L'Huillier *et al.*(1984) reported Coopworth ewes consumed 36% more prairie grass pasture than ryegrass pasture when both species were offered the same allowance at a similar pasture height. During summer, the difference was 87%. Differences in the spatial distribution of green leaf within the swards were likely to have been responsible for the difference in intake.

For Prairie grass, 36% of green leaf was greater than 3 cm above ground level compared with 5% for ryegrass. Differences in allowance-liveweight gain relationships between different pasture species (Figure 2.5) are likely to partly reflect differences in the spatial distribution of green leaf.

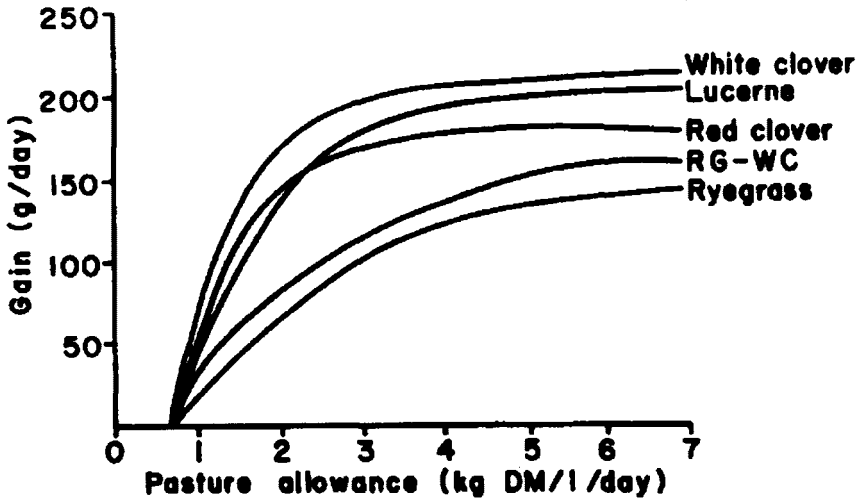


Figure 2.5. *The effect of pasture species on the relationship between pasture allowance and daily liveweight gain of lambs at pasture (from Jagusch et al., 1979b).*

In addition to this effect, intake may decline at high pasture masses as animals attempt to preferentially select green over dead material (Hawkins *et al.*, 1993) and leaf rather than stem (Poppi *et al.*, 1987).

Body size

The allometric model of Illius and Gordon (1987) identified body size as a factor affecting the ability to obtain adequate energy intake from short pastures. Small animals (30 kg) were able to achieve intake equivalent to twice maintenance at a pasture height of 2.3 cm compared with a large animal (120 kg) which only achieved a maintenance intake. Increasing pasture height from 2 to 7 - 8 cm increased the difference between relative intake of large and small animals. The implication of this is that longer pasture may need to be provided to large elk-type deer to achieve a similar intake compared with smaller red deer.

Thompson and Parks (1983) showed large sheep breeds had a higher intake than smaller breeds based on results from long-term feeding and growth experiments. Large rams ate more than small rams at any age. However, after scaling for mature weight (Taylor, 1980), there was little difference in feed intake between large and small rams. The implication to this study is that hybrid deer may eat more because of their larger mature size.

Species of grazer

The general relationship between pasture allowance and intake is similar for lambs (Thompson and Jagusch, 1977; Jagusch *et al.,* 1979b), cattle (Marsh, 1977; Jamieson and Hodgson, 1979), lactating dairy cows (Bryant, 1980), pregnant ewes (Rattray *et al.*, 1982a), ewes with lambs (Rattray *et al.*, 1982b) and young red deer (Adam and Asher, 1986). While the general form of the response curve is similar for different animal species and different physiological states there is much variation in the actual intake response curve to increasing pasture allowance. For example, maximum intake was only achieved where allowances were 3.5 times the maximum intake in calves (Jamieson and Hodgson, 1979), 4 times maximum intake for dairy and beef cattle (Holmes, 1987) and 4 - 5 times maximum intake for sheep (Gibb and Treacher, 1976; Hodgson, 1984).

In addition to pasture allowance and pasture mass, preference for one or more pasture species within a mixed sward and/or selection of plant components within a pasture species varies between and within animal species. For example, sheep select diets with a higher proportion of green material and a higher nutritive value than cattle (Jamieson and Hodgson, 1979) and goats are known to harvest more grass and less clover compared with sheep grazing similar mixed swards (Clark *et al.*, 1982). Although there is not a good understanding of how these differences occur it is likely harvesting technique, shape of mouth, and feed demand may all be contributing factors.

Differences between deer species have been reported. Grazing patterns of red and sambar deer were similar for total grazing time, rumination but timing of grazing (night vs day) and prehending biting rate which may indicate differences in bite weight and grazing selectivity (Semiadi, *et al.*, 1993) differed between the species.

Specific pasture allowance intake relationships for deer

There are few experimental data which specifically describe the relationship between pasture allowance and intake or liveweight gain for deer and presumably farmers have used sheep guidelines when allocating pasture to deer.

Hamilton *et al.* (1998) showed liveweight gain of stags continuously stocked over the summer did not increase beyond a pasture height of 6 cm. (Figure 2.6).

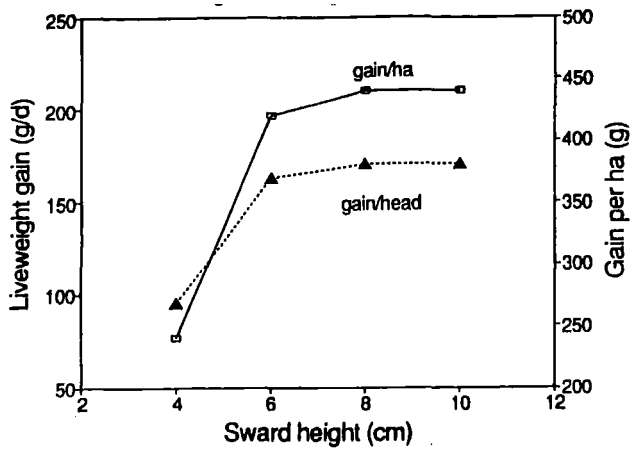


Figure 2.6 *Liveweight gain response of yearling red deer stags to pasture height during summer (from Hamilton et al., 1995).*

Of the few experiments conducted in a rotational stocked system, the work of Adam and Asher (1986) with red stags (Figure 2.7) is unique in that it describes liveweight gain over a range of allowances (2 -7 kg DM/h/day). More recent work (Ataja *et al.,* 1990; Ataja *et al.,* 1992; Semiadi *et al.,* 1993a; Kusmartono, 1995) have tended to concentrate on the plateau region of the relationship by either offering generous pasture allowances or a high post-grazing pasture mass. Consequently, there is little information on the effect of less generous pasture allocation more commonly found on commercial farms.

Deer are known to have a pronounced seasonal cycle of feed intake (Kay and Goodall, 1976) characterised by high intake in spring and summer and lower intake in autumn and winter. A different response of intake to pasture allowance at similar times of the year is a possible consequence of different seasonal cycles of feed intake between sheep and deer.

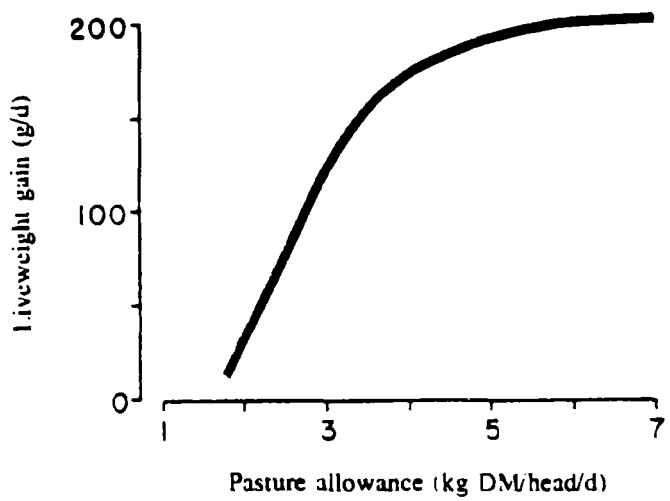


Figure 2.7. *The liveweight gain response (g/day) of red weaner stags to changes in pasture allowance (kg DM/head/day) in autumn (from Adam and Asher, 1986).*

For deer, the relative liveweight gain advantage hybrid deer have over red deer was reduced when pasture allowance declined between two years (Simpson, unpublished data). This farm-based data is evidence of a different response to pasture allowance between these genotypes although care should be taken in the interpretation of this observation as there may be many other confounding factors. However, the suggestion is that animals with increased physiological drive or potential may differ in their response to increasing pasture allowance as previously hypothesised for cattle by Ferrell and Jenkins (1985).

Summary

Deer respond to variation in pasture allowance and pasture height in a similar fashion to sheep and cattle although the exact shape of the response relationship for rotational grazing, with the exception of autumn, is currently unquantified. There is some evidence that species (cow vs sheep) breed (Friesian vs Jersey) and genetic merit (high vs low BV cows) influence the intake response to pasture allocation and show different levels of intake or production at a common pasture availability. It is possible therefore, that hybrid and red deer could differ in their intake response to pasture allocation.

The following section considers evidence for variation (between genotypes) in digestibility, metabolisability and efficiency of utilisation.

2.2 Energy metabolism

Introduction

Red and hybrid deer could differ in their level of production from the same gross energy intake if;

(1) the proportion of ME in GE was greater in one genotype due to digestibility or metabolisability differences and/or
(2) ME requirements for maintenance were higher for one genotype compared with the other and/or
(3) the energy available for fat and protein deposition was used with a greater efficiency for one genotype compared with the other and/or
(4) the energy value of the gain (ratio of fat:protein) was different between genotypes.

Digestibility

Differences in digestibility between different breed or genotype of animal may be due to

1) selecting a more digestible diet from the same pasture on offer or
2) digesting more or less of the same diet resulting from a faster or slower degradation and or passage rate.

In general, sheep tend to select a diet containing a higher proportion of green leaf and less stem and dead material than is in the pasture (Rattray and Clark, 1984). A similar, but less pronounced, pattern exists with cattle (Forbes and Hodgson, 1985). Factors which determine the components of forage selected include (i) ease of eating which increased intake rate (Kenny and Black, 1984) , (ii) sensory factors relating to taste, odour and tactile stimulation of feed (Colebrook *et al.,* 1985, 1990), (iii) water content of the forage (Black *et al.,* 1987) and (iv) the quantity and spatial distribution of components within a sward (Hodgson, 1985; Forbes, 1988). Taylor *et al.* (1987) suggested that incisor arcade breadth influences the amount of forage ingested per bite, the minimum distance between components for effective discrimination and maximum eating rate.
While this could explain largely why cattle are less able to discriminate between forage components than sheep (Forbes and Hodgson, 1985) there is no evidence to suggest two genotypes of deer differ in their ability to select components from pasture.

Apparent digestibility of DM and energy is affected by ruminant species. Although digestibility of roughage diets is to a large extent dependant on the chemical components of feed, different ruminant species do show small differences in their ability to digest a common feed. For example, goats have been shown to digest fibre more effectively than sheep, particularly when fed low quality roughage (Howe *et al.,* 1988; Domingue *et al.*, 1991a). Further, on a diet of lucerne hay in winter, apparent DM digestibility was lower for deer (63%) than for goats (72%), with sheep (67%) being intermediary.

Sheep and cattle appear to digest silages, forages and concentrate diets with similar efficiency (Wainman, 1977).

Webster *et al* (1974) reported a non-significant trend for Angus (66%) steers to digest a pelleted barley based diet to a greater extent than Friesians steers (63%). Iason *et al.* (1995) found the apparent digestibility of dry matter, organic matter, nitrogen, NDF and ADF were lower for Shetland ewes during winter on a hay diet compared with either Scottish Blackface or Dorset Horn. Genotype effects on digestibility may be seasonally dependant. An increase in the level of feed intake generally reduces digestibility therefore species like deer which have a big seasonal change in intake may show a seasonal change in digestibility compared with sheep. There is some evidence for this (Domingue *et al.,* 1991a). Further, if deer genotypes differ in the seasonal amplitude of intake, it is possible seasonal variation in digestibility may also occur.

Metabolisability

The metabolisability of digestible energy reflects the loss of methane and urinary energy from the animal. Methane is a product of microbial degradation of feed in the rumen and represents an energy loss to the animal and typically 5 - 9% of gross dietary energy (Blaxter and Clapperton, 1965). Methane yield correlates negatively with DM intake (Blaxter & Clapperton, 1965; Gibbs *et al.,* 1989). Lower methane yields at high intakes are presumably a reflection of faster rumen clearance and thus proportionately lower rumen digestion of feed. However, Uylatt *et al.*(1997) showed methane emission was only weakly correlated with DM intake suggesting DM intake was a relatively minor determinant of variation in methane emission. For both sheep and cattle, inter-animal variation was the main source of variance in methane emission (87%) but currently there is little evidence for systematic differences between breeds and species.

Urinary losses represent about 12% of digestible energy and differences between species (deer and sheep) are relatively minor (Simpson *et al.,* 1978b) but energy loss through urine does increase with high protein diets.

It is unlikely therefore that red and hybrid deer differ in productivity based on metabolisable energy differences.

Maintenance Energy Requirements

There are two ways of estimating the maintenance energy requirements (ME_m) of an animal.

1) regression of ME intake (above or below ME_m) on energy retention in the body or more often liveweight change. The value of ME intake at zero energy or zero liveweight change is considered ME_m
2) the component energy costs of maintenance are measured and accumulated factorially to provide an estimate of ME_m when the efficiency of utilisation of ME_m for maintenance is known. For example,

$$ME_m = \frac{\text{(Fasting heat production + cost of eating (and ruminating) + cost of walking)}}{k_m}$$

Only the first approach has been used to estimate the ME_m for species of deer (Table 2.1).

Table 2.1 *Energy (MJ ME/$W^{0.75}$/day) required for maintenance of liveweight (ME_{W0}) or energy (ME_{E0}) for housed and free ranging deer genotypes in winter, spring and summer.*

Species*	Age (months)	Season	Environment	ME_{E0} MJ ME/$W^{0.75}$/day	ME_{W0} MJ ME/$W^{0.75}$/day	Authors
wapiti	5	winter	free ranging		0.56	Cool & Hudson, (1996)
wapiti	6-14	winter	housed		0.47	Jiang & Hudson, (1994)
wapiti	24	winter	housed		0.57	Jiang & Hudson, (1992)
wapiti	6-14	spring	free ranging		0.90	Jiang & Hudson, (1994)
wapiti	6-14	summer	housed		0.73	Jiang & Hudson, (1994)
wapiti	24	summer	free ranging		0.94	Jiang & Hudson, (1992)
red deer	adult	winter	housed		0.53	Brockway & Maloiy, (1968)
red deer	6-20	winter	housed		0.57	Fennessy *et al.* (1981)
red deer	6-20	winter	free ranging		0.85	Fennessy *et al.* (1981)
red deer	6	winter	housed	0.45		Simpson *et al.* (1978b)
red deer	5-17	year	housed		0.52	Suttie *et al.* (1987)
red deer	6	summer	housed	0.50		Simpson *et al.* (1978b)
red deer	10-14	summer	housed		0.57	Semiadi *et al.* (1998)
sambar	10-14	summer	housed		0.47	Semiadi *et al.* (1998)
white tailed	adult	winter	penned outside		0.67	Ullrey *et al.* (1970)

** Wapiti is the North American term for elk*

Estimates of the energy required for maintenance have generally been derived using two methods. The most widely used method is to determine the amount of energy required to maintain zero weight change (to estimate ME for liveweight maintenance). The requirement MJ/$W^{0.75}$ /day defined as the intercept value of the best fit linear relationship fitted to MEI (MJ/$W^{0.75}$/day) and liveweight gain (g/day) data. Alternatively other authors (Simpson *et al.*, 1978b) have estimated maintenance requirements based on respiratory gaseous exchange using closed circuit respiratory calorimeters to calculate ME for zero energy retention.

The requirements for maintenance for red deer reported in Table 2.1 are similar to the ARC (1980) estimates for cattle but between 30 and 50% higher than those of sheep. Only suggestions can be made as to any systematic variation of estimates made under different circumstances but the crude mean for red deer is 0.57 MJ/$W^{0.75}$ /day and for elk is 0.69 MJ/$W^{0.75}$ /day, for housed deer is 0.57 MJ/$W^{0.75}$ /day and for free ranging deer is 0.78 MJ/$W^{0.75}$ /day and for winter is 0.54 MJ/$W^{0.75}$ /day and for spring/summer 0.69 MJ/$kg^{0.75}$ /day.

In the only comparison between deer species under similar conditions, (Semiadi *et al.*, 1994) young sambar deer (*Cervus unicolor*) were reported to have a lower requirement for maintenance (0.47 MJ ME/$W^{0.75}$ /day) compared with red deer (0.57 MJ ME/$W^{0.75}$ /day). As a consequence, at any particular rate of intake sambar retained more energy than red deer. The lower ME_m was reported to be a logical explanation of a greater feed conversion efficiency of sambar stags and hinds (11.4 kg DM intake/kg LWG) compared with red deer stags (14.3 kg DM intake/kg LWG). A lower energy requirement for both maintenance and liveweight gain in sambar deer (tropical-type) was suggested as an adaptive strategy to reduce unnecessary heat production in a hot climate. For red deer, which have evolved in a temperate climate, higher levels of heat production may be beneficial in cooler conditions.

There are no comparisons of maintenance requirement between red deer and red x elk hybrids and it is difficult to compare data for red deer and wapiti (elk) since they involve separate experiments run under different conditions. Comparison of ME_m for red deer and hybrids under similar conditions would provide novel information and may help to explain differences in liveweight gain.

Difference between red deer and elk run under the same conditions which could be due to a difference any one or more of the following

1) Fasting heat production (FHP)
2) Costs and/or level of activity
3) Efficiency of utilisation of ME for maintenance (k_m)
4) Lower critical temperature

Fasting heat production

The concept of a basal metabolic rate (most often measured as a rate of heat production under standardised conditions) has been used to compare metabolic rate between and within species. Basal metabolic rate can be defined as the heat produced by an animal when in a resting, post-absorptive state in a thermo-neutral environment. However, the term fasting heat production (FHP) is better used to describe the situation more commonly found in ruminant animals where they are fasted and in a thermo-neutral environment but heat production is elevated by some voluntary muscle activity (as complete relaxation in livestock is rarely achieved) and by digestion (as a completely post-absorptive state is not easily achieved in ruminant animals). Fasting heat production is the major component of ME_m, and arguably differences which occur in ME_m are likely to originate, at least in part, from FHP. The following section reviews factors affecting FHP.

Factors affecting FHP

Body size

The initial studies of Kleiber (1932) and Brody and Procter (1932) and later work of Zeuthen, (1947); Zeuthen (1953), Hemmingsen, (1950) and Hemmingsen (1960) showed that for many animals FHP was proportional to body weight raised to the power of 0.75 (Figure 2.8). This is an interspecies relationship and the exponential function for different groups of animals of different taxonomic grouping can vary from 0.60 to more than 0.90 (Calder, 1987).

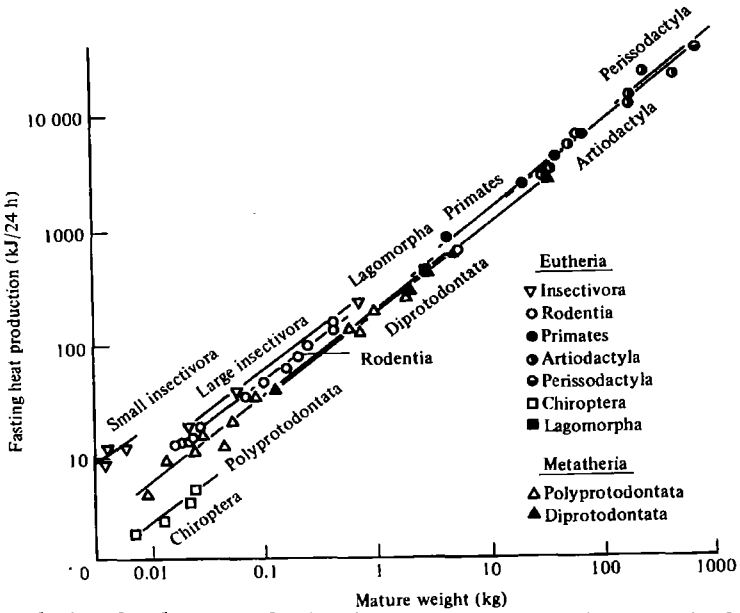


Figure 2.8 *The relationship between fasting heat production and mature body weight for species within different taxonomic groups indicating fasting heat production increases with* $W^{0.75}$ *(from Blaxter, 1989).*

Species

Although taxonomic grouping does explain some of the variation in FHP there is evidence that breeds within a species may differ in FHP. Sheep have a lower and cattle a higher FHP compared with the inter-species mean and even the mean for ungulates (Blaxter, 1989). There is also some evidence that genotypes within a species may differ with higher values associated with more productive breeds at any given weight (Figure 2.9).

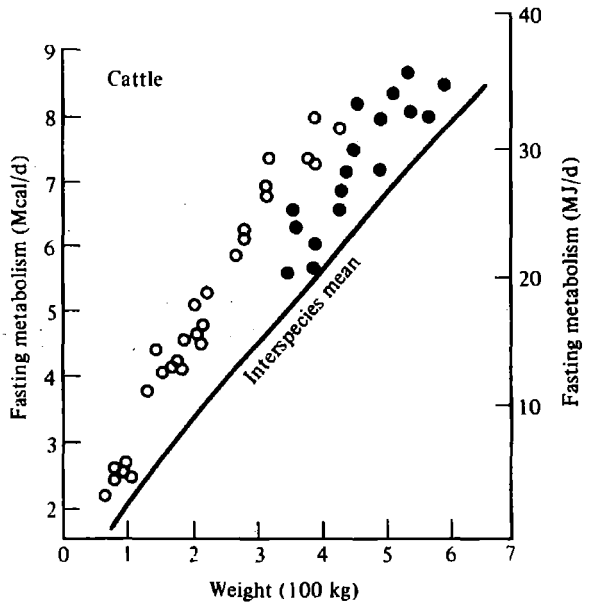


Figure 2.9 *The relationship between body weight and fasting heat production for Ayrshire (O) and Aberdeen Angus (●) cattle and their relationship with the inter-species mean (from Blaxter, 1989).*

Nutritional status

Although fasting heat production by definition is measured in a post-absorptive state (requiring short term starvation to achieve this), previous nutritional history has a significant effect on fasting heat production. For example, sheep that lost significant amounts of fat and protein after being offered half the feed required for maintenance, showed a reduction in fasting metabolic rate from 265 to 231 $kJ/W^{0.75}$ /day (Marston, 1948).

Under-nutrition is known to have a negative effect on weight of internal organs including liver (Koong and Ferrell, 1990) and intestines (Burrin *et al.*, 1990). Webster (1981) has suggested that gut and liver combine to contribute about 40% of total heat production in sheep and consequently reducing the weight of these organs is likely to reduce FHP. It would follow that animals offered high levels of nutrition may have elevated levels of fasting heat production due to the increased size of internal organs with high energy demands.

Deer showed marked seasonal variation in feed intake and therefore, FHP could be expected to be lower during winter when feed intake is reduced compared with spring/summer when intake increases. There is some evidence that FHP is lower in winter than in spring. For example, where intake increased from winter to summer for wapiti (Jiang and Hudson, 1993), summer FHP tended to be higher in spring compared with winter although the differences were not significant. Further, FHP was lower in winter than during summer (Silver *et al.*, 1969) in white tailed deer. However, it is unclear whether this is a seasonal effect *per se* (Silver *et al.*, 1969) or a reflection of the seasonal cycle of intake (Nilssen *et al.*, 1984; Pekins and Kanter, 1992).

Activity

The energy cost of activity could differ between genotypes if 1) the costs of activity (grazing, walking, standing) were different or 2) the amount of activity differed.

Costs of walking and grazing do not differ markedly between species when expressed per unit of body weight (Blaxter, 1998). Therefore, it is unlikely that activity cost contribute to any differences between genotypes.

The amount of activity largely depends on feed availability since activity associated with the harvest of feed is a large proportion of total activity. It is unlikely, if animals are compared under similar grazing environments that differences in grazing activity are significant.

Homeothermy

There is some evidence that deer differ from other species in the environmental temperature below which they expend energy on thermogenesis (reach their lower critical temperature) (Simpson *et al.*, 1978a), thus increasing maintenance requirement. There is also evidence that deer species originating from tropical and temperate environments may differ in heat production at maintenance (Semiadi *et al.*, 1994). It has been suggested lower ME requirements for both maintenance and growth in tropical-type animals may be an adaptive strategy to counter high environmental temperatures. On the other hand, higher levels of heat production may be needed to counter the lower ambient temperatures experienced by red deer in the temperate zone. However, it is unclear whether two temperate species and furthermore a hybrid and pure bred of two temperate species differ significantly in maintenance heat production.

Summary

From previous studies, there appears to be variation in maintenance requirement between red deer and wapiti but species effects are confounded by age, season, environment and method of estimation. Where deer species have been compared directly, temperate and tropical species differ in their requirement for maintenance, possibly as a strategy to counter high environmental temperatures. However, it is unclear if temperate deer species differ in their maintenance requirement.

The factors which combine to make up ME requirement for maintenance are FHP, the efficiency of ME used for maintenance (k_m), energy required for activity and energy associated with thermogenesis. It is likely differences in ME_m are reflected in FHP since FHP is a major component of ME_m. However it is unclear whether genotypes differ in amplitude or timing of any seasonal cycle of FHP which may exist or differ in FHP *per se*.

ME intake is distributed between ME_m and ME_p (energy requirement for production). Regardless of any differences between genotypes in ME_m, a difference in the efficiency with which each genotype utilises ME for liveweight gain could explain differences in liveweight gain. The following section outlines the factors affecting the utilisation of ME for liveweight gain.

Efficiency of utilising ME for liveweight gain

The energy cost of liveweight gain can be determined from the regression of energy retention in the body or more often liveweight change on ME intake (above ME_m). The value of the regression co-efficient is considered to be the energy cost of liveweight gain. Previous estimates of the cost of liveweight gain for both red deer and wapiti and for hinds and stags, using this method are given in Table 2.2.

Table 2.2. *Previously published estimates of the energy costs of liveweight gain in deer.*

Genotype	Sex	Energy cost (MJ ME/kg)	Author
Wapiti	Stags	33.4	Wairimu *et al.* (1992)
Wapiti	Stags	38.5	Jiang and Hudson (1992)
Red	Stags	37.0	Fennessy (1981)
Red	Stags	38.4	Semiadi *et al.* (1994)
Red	Hinds	55.0	Suttie *et al.* (1987)
Red	Hinds	46.9	Semiadi *et al.* (1994)

Previously published estimates for the energy costs of liveweight gain are similar for young red deer and wapiti stags, but estimates are much higher for hinds. Presumably, the energy value of the gain is higher for hinds as a result of a greater proportion of fat in gain compared with stags of the same age. The requirement for energy gain can be described as;

$$ME_g = \frac{EV_g \times LWG}{k_g}$$

(where ME requirement for energy gain is in MJ ME/kg, EV_g is the energy value of the gain in MJ ME/kg and k_g is the efficiency of utilisation of energy for energy deposition)

Genotypes could potentially differ in the efficiency of utilisation of energy for liveweight gain if;

(1) liveweight gain contained a different proportion of fat and protein for each genotype (ie. genotypes had a different composition of gain) and/or

(2) inherent differences existed in the efficiency with which fat and protein were deposited

There is variation in the efficiency with which ME is deposited with energy retained as fat being much more efficient (approx. 0.7) than energy retained as protein (approx. 0.3) (McDonald *et al.*, 1995). The following section reviews previously published values for the cost and efficiency of fat and protein deposition and factors affecting them and also examines the factors affecting the composition of gain in young growing animals

The contrasting concentration of energy contained in fat and protein potentially enables variation in efficiency of liveweight gain through a different composition of gain. Fat contains almost twice (39.5 MJ ME/kg) the amount of energy per kg DM than protein (23.4 MJ ME/kg) (Rattray and Joyce, 1976). In addition, protein is deposited in the body with additional cellular water such that hydrated protein is about 25% protein and 75% water (Sykes and Nicol, 1983). The energy content of hydrated protein therefore is approximately 6.0 MJ ME/kg. Consequently there is much less energy contained in 1 kg of protein tissue than in the same amount of fat tissue. From a liveweight gain point of view, individuals accumulating liveweight which is predominantly protein (young growing animals) will have a greater liveweight gain per unit of energy partitioned to growth than those with a higher proportion of fat in the liveweight gained (more mature animals). The effect that the near six fold difference in energy content of gain has on the relationship between composition of gain and rate of liveweight gain is tempered somewhat by the efficiencies of fat and protein deposition (high for fat, low for protein) but nonetheless protein gain requires somewhat less energy than fat gain.

For example,

$$\frac{39.5 \text{ MJ ME/kg}}{0.7} = 56.4 \text{ MJ ME/kg} \quad \text{vs} \quad \frac{6.0 \text{ MJ ME/kg}}{0.3} = 30 \text{ MJ ME/kg}$$

Efficiency of utilisation of ME for fat and protein deposition

The energy cost of fat deposition (between 40 - 60MJ ME/kg) is the energy cost associated with 1 kg of adipose tissue since adipose contains insignificant amounts of water. The synthesis of protein probably requires only 3 - 13 MJ ME/kg (Webster *et al.*, 1980) but net protein accretion is the result of protein synthesis and degradation and therefore considerably more protein is synthesised than is actually deposited thereby increasing the real cost of depositing protein to as high as 78MJ ME/kg (Orskov, 1976, Webster, 1980). The partial efficiency by which fat (k_f) and protein (k_p) are deposited is estimated from the regression coefficients of a multiple regression relating MEI to protein and fat retention ($g/W^{0.75}$).

The energy cost of depositing fat and protein differs. The energy costs of deposition are associated with the biochemical reactions involved in the net accretion of tissue. Estimates of the ME cost and efficiency by which fat and protein are deposited are given in Table 2.3.

Textbook values for the efficiency of energy deposition as fat and protein are given as 0.7 and 0.3, respectively (Sykes and Nicol, 1983) but there is considerable variation across individual experiments measuring efficiency (Table 2.3). It is unclear whether the variation in results above reflects variation in diet, age, breeds or is just random.

Table 2.3 *Estimates of the ME cost and efficiency of fat and protein deposition in different species of animals offered different diets.*

Animal	Author	Fat		Protein	
		MJ ME/kg	k_f	MJ ME/kg	k_p
Milk-fed calves	Donnelly (1975)	37	1.00	65	0.36
Milk-fed lambs	Kielanowsky (1965)	63	0.61	30	0.78
Weaned lambs (4-5 weeks old)	Orskov and McDonald (1970)	48	0.80	68	0.34
Lambs 6 months (conc. feed)	Rattray *et al.* (1974)	43	0.89	191	0.12
Lambs 6 months (conc. feed)	Rattray and Joyce (1976)	49	0.80	120	0.15
Mixed age ewes	Olthoff *et al.* (1989)	12	1.00	40	0.59
Ruminants	Blaxter (1989)		0.79		0.45

In young ruminants the development of rumen function coincides with a reduction in efficiency of utilisation of ME. Very low efficiency of utilisation of ME for fat and protein deposition in young ruminant lambs compared with pre-ruminant lambs have been reported (Fennessy *et al.*, 1972).

When comparing species across a number of experiments there appears to be considerable variation, but nutrition, environment and experimental design are likely to be confounding factors. Where experiments have aimed to compare efficiencies of fat and protein deposition between breeds (Wurgler and Bickel, 1986; Olthoff *et al.*, 1989) large variation between individuals has resulted in a pooled analysis across breeds and therefore it is unclear whether breed exerts a significant effect. The variation which occurs between individuals may be a result of the high inter-correlation between fat and protein deposition. In such situations where two independent variables are highly correlated a multiple regression model is not a good approach.

The efficiency of utilisation of ME for fat and protein deposition is affected by diet, species and stage of development and there appears to be considerable variation in estimates between individuals It is likely that differences between red and hybrid deer, if any, are small and would be difficult to measure.

Composition of gain

As an animal increases in liveweight (growth) its body changes in the proportional distribution of parts (limbs, trunk, head) and tissues (adipose, lean and bone). Such changes represent development and reflect stage of maturity. These relative changes in body composition were first expressed mathematically by Huxley (1924) and it is now standard practise to express the relationship as a body part to the whole body by way of allometric equation which conventionally expresses curvilinear relationships in the linear form;

$$\text{Log } y = \log a + b \log x$$

(where y is the body part, x is the weight of the whole body, b is known as the relative growth coefficient of x to y and a as the constant).

Relative growth coefficients less than 1.0 for tissues such as bone define early maturing components and those greater than 1.0 for tissues such as fat indicate late maturing components. These allometic equations explain the changes in body composition with maturity and thus changes in the composition of gain as animals mature.

These relationships appear to be robust and are difficult to disrupt. However, there is some evidence that potential differences in the relative growth of tissues may arise from ;

1) differences in the rate of liveweight gain
2) dietary imbalances
3) photoperiod

Rate of liveweight gain

There is some evidence that rate of liveweight gain may affect the composition of liveweight gain although there is by no means a consensus of opinion and further any effect could be confined to certain species. For example, Black (1974) presented evidence of body composition changes in lambs relating to various rates of liveweight gain resulting from different nutritional treatment but Greenhalgh (1986) concluded that nutrition had a minor effect on body composition in sheep. Pleasants *et al.* (1998) concluded that rate of liveweight gain as a result of nutritional manipulation lead to differences in carcass composition for cattle. However, ARC (1980) and Theriez *et al.* (1982), proposed that body composition was not affected by rate of growth.

Overall there is more evidence of a liveweight gain effect on the composition of liveweight gain for cattle than for sheep but currently no evidence either way for deer.

Dietary imbalances

There is considerable evidence in the literature that increasing protein intake or absorption can affect the composition of liveweight gain. For example, Andrews and Orskov (1970) and Orskov *et al.* (1976) grew lambs on diets which varied in dietary protein concentration (10 - 20%). At the same liveweight, lambs on low protein diets deposited more fat and less protein in liveweight gain than lambs on higher protein diets.

Not only is the total amount of dietary protein important in the composition of gain but the quality of protein is also important. Proteins containing an imbalance in amino acids reduce the efficiency by which dietary protein is utilised for protein deposition. In ruminants, methionine followed by lysine, arginine and histidine are considered the most limiting amino acids. An illustration of the effect of supplementing with limiting amino acids was provided by Barry (1981). Abomasal infusions of casein and methionine to lambs, increasing in liveweight from 16 to 24 kg deposited more protein and less fat in the carcass compared with non-infused controls.

Photoperiod

Forbes *et al.* (1979) and Forbes *et al.* (1981) suggested that long day length (8 h dark - 16 h light) stimulated the growth of non-fat tissues at the expense of fat in young lambs and Philips *et al.* (1997) found steers under a natural lighting regime (average 9.7 h/day) produced carcasses with a higher fat content than steers kept in conditions where day length had been artificially extended to 16h/day. However, neither Francis *et al.* (1997), Eisemann *et al.* (1984) or Schanbacher and Crouse (1980) measured any consistent effect of day length on body composition. While there is some evidence that photoperiod may change the composition of liveweight gain in young growing animals, results from current research are variable and inconsistent between experiments. It is possible, given the large

effect of photoperiod on intake and liveweight gain in deer relative to sheep and cattle, that any effect of photoperiod on body composition may be larger and therefore more easily measured in deer.

Summary

Currently, there is little evidence in the literature to suggest red deer and elk differ markedly in the cost of liveweight gain although this needs testing in a common environment. Further, it is unlikely differences occur in the efficiency of energy for energy deposition as fat or protein. However, it would be expected that elk given that they are later maturing would have lower protein : energy ratio in gain at the same age.

2.4 General summary of the literature and outline of thesis

Elk have a greater mature liveweight than red deer and this difference in maturity might be expected to explain differences between red deer and red deer x elk genotypes. For example, relative to red deer, red deer x elk hybrids would be expected to show;

- greater daily liveweight gain and greater absolute daily intake
- relatively lower intake when offered short pastures
- a lower proportion of fat in liveweight gain
- a leaner body composition at any given body weight

However, the literature does not suggest that genotypes would show differences in;

- FHP, or seasonal changes in FHP, activity or lower critical temperature
- efficiency of utilisation of ME for maintenance, or for protein of fat deposition
- digestibility of a common feed source

However, there is little data to quantify those features of the two genotypes which might be expected on theoretical grounds to differ, or to confirm that those which the literature suggests would not differ, do in fact not differ. This thesis sets out to address some of these issues

The proposed course of study is set out in Figure 2.10. A grazing experiment will be the starting point for this research (Stage I) to test the hypothesis that red deer and hybrids differ in their liveweight gain response to pasture allowance. If apparent intake proved to explain differences in liveweight gain between genotypes this study was planned to shift focus to defining a range of intake pasture allowance relationships for each genotype.

Assuming differences in intake was unable to explain differences in liveweight gain between genotypes a comparison of energy metabolism was to be undertaken (Stage II) testing the hypothesis that red and hybrid deer differ in their ability to digest or metabolise a common feed and/or in their requirement for zero energy balance and/or in the efficiency of utilisation of energy for liveweight gain and/or in the composition of gain.

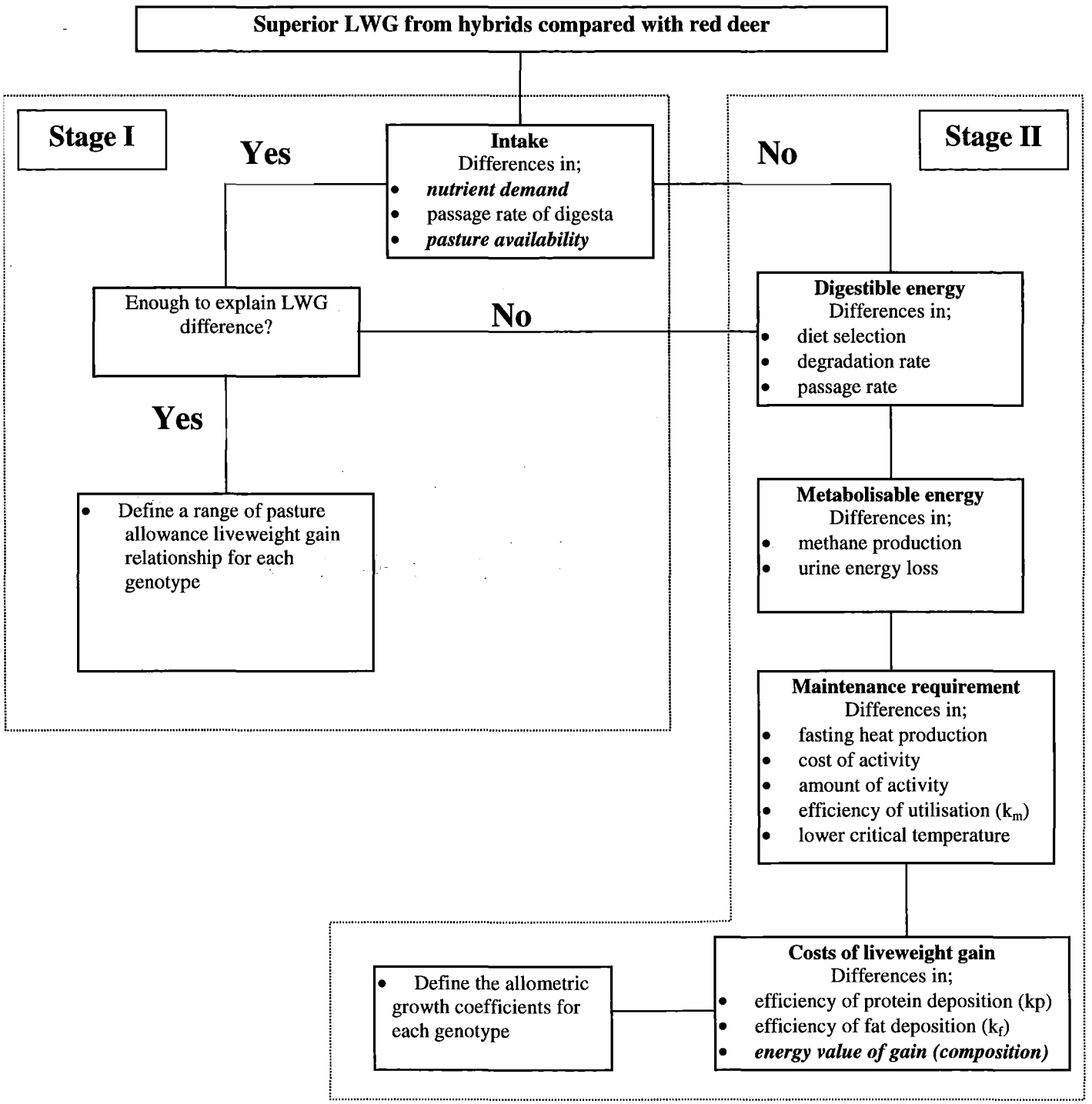


Figure 2.10 *The proposed experimental model to investigate the relative contribution of various factors to the liveweight gain difference between red and hybrid deer. The proposed course of study would begin with a field experiment (Stage I) and progress to a comparison of the components of energy metabolism (Stage II). Components in italics represent those for which there is evidence that genotypes could differ.*

Chapter 3

Effect of pasture availability on the seasonal liveweight gain of young red deer *(Cervus elaphus)* and red x elk hybrid stags.

3.0 Introduction

In most environments, red x elk hybrid (hybrid deer) weaner stags increase liveweight at a greater rate in the 12 month period post-weaning and are heavier at 12 months of age compared with red deer stags (Drew and Hogg, 1990; Walker *et al.,* 2000). However, farm-based observations suggest the relative advantage in liveweight gain to hybrids over red deer is reduced in environments where pasture intake is restricted (Simpson, unpublished data). This indicates a genotype x nutritional environment interaction that would have implications for (a) the choice of genotype for environments that differ in their ability to supply pasture and (b) the appropriate feeding levels for different genotypes.

The influence of pasture allowance on grazing intake (and animal production) has been examined in many species. Pasture allowance-liveweight gain relationships for ewes in mid-pregnancy (Jagusch *et al.,* 1981; Hawker, 1987) late pregnancy (Rattray *et al.*, 1982a) lactation (Rattray *et al.*, 1982b) for lambs (Jagusch *et al.*, 1979a), hoggets (Hawker *et al.*, 1985), beef cattle (Marsh, 1977; Reid, 1986), dairy cattle (Holmes *et al.,* 1979; Bryant, 1980) and goats (McCall and Lambert, 1987) have all been established. However, there are few experimental data on pasture allowance-intake relationships for deer. The work of Adam and Asher (1986) has shown an increase in liveweight gain between 2 and 7 kg DM/head/day during the autumn but in recent work (Ataja *et al.*, 1992; Semiadi *et al.*, 1993a) single, generous pasture allowances (7 - 8 kg DM/head/day) have been offered providing little information on pasture allowance - liveweight gain relationships when pasture supply is restricted.

The primary aim of the experiment described here was to compare the liveweight gain of red and hybrid stags over a range of pasture allowances in winter, spring and summer.

3.1 Materials and Methods

Experimental design

The experiment took place at the Lincoln University Deer Research Unit, Canterbury, New Zealand. The aim of the experiment was to compare the winter, spring and summer liveweight gain of red and hybrid deer over a range of pasture allowance and pasture mass typically found on farms. Groups of red and hybrid weaner stags were rotationally stocked on ryegrass (*Lolium perenne*)/white clover (*Trifolium repens*) pasture during winter (21 June - 15 August), spring (12 October - 14 December) and summer (25 January - 28 March) of 1994 - 95 (experimental periods). In each experimental period, groups of deer (10 - 12) were offered one of four pasture allowance-pasture mass combinations. Liveweight gain was determined by weighing animals weekly.

Animals

Forty eight red weaner stags with a pre-trial liveweight of 57.4 ± 2.0 kg (mean ± S.D.); and forty eight hybrid weaner stags of pre-trial liveweight 68.0 ± 2.2 kg (mean ± S.D.); all approximately 7 months old, were used in the experiment. These were selected from deer that were sourced in equal sized groups (14 animals /group) from 8 different commercial properties from around the Canterbury region. Deer arrived one month prior to the beginning of the experiment and were exposed to temporary electric fencing and yarding facilities to allow familiarisation with experimental routines. Deer ran as a single herd during this period on typical autumn ryegrass/white clover pasture.

To establish formally the degree of hybridisation, all animals were blood typed (Tate *et. al.*, 1988). Animals were segregated on genotype-specific blood protein genetic markers using a commercial blood typing service. For red deer, genetic markers showed no evidence of hybridisation while hybrids were found to be on average a 35:65, elk:red hybrid.

Deer received a moxidectin anthelmintic (18 ml, Vetdectin, Cyanamid NZ Ltd) on arrival and were re-dosed if faecal egg counts rose above 500 eggs/g. In addition, deer received a yersiniosis vaccine (5 ml s.c. Yersinia vax, Agvax Developments Ltd) and a further supplementary dose 6 weeks after the initial injection. All deer were supplemented with copper using a 5 g copper oxide needle containing bolus (Copacaps, Rhone Merieux).

Treatment groups

Prior to each of the three experimental periods (winter, spring, summer), deer within each genotype were divided into 4 groups. Within each genotype, groups contained similar numbers of deer from each source, were similar in mean liveweight and within-group variation in mean liveweight. Not all stags were involved in the experiment and surplus stags were run together with commercial animals

of the same age on typical ryegrass/white clover pasture. Allocation of deer to groups during the spring and summer experimental periods was also balanced for previous nutritional treatment. The number of deer per group for winter, spring and summer periods was 10, 12 and 10, respectively.

For each experimental period, two groups (one of each genotype) were assigned to each pasture allowance-pasture mass combination. Red and hybrid groups grazed the same pasture (same paddock) in adjacent breaks. Deer were confined to weekly prescribed grazing areas using a combination of temporary 5 wire and netting electric fencing (Plate 3.1). Individual animal liveweight (to the nearest 0.1 kg) immediately off pasture was recorded weekly using a deer crush mounted on load bars (Tru-test, model 700 economy plus, Tru-test Distributors Ltd, Auckland).

Plate 3.1. A *group of red deer (left) and hybrids (right) confined by temporary electric fencing to a grazing area providing 4 kg DM/W$^{0.75}$ /day on a 3000 kg DM/ha pasture in a rotationally stocked system during spring.*

Pasture allocation

Pasture was allocated on the mean metabolic liveweight ($W^{0.75}$) of each group. Allocations were at one of four pasture allowances designed to cover a wide range (Table 3.1). Low allowances were designed to produce positive but minimal liveweight gain and high allowances were set so that pasture mass would not limit liveweight gain.

Table 3.1. *Pasture allowance (kg DM/$W^{0.75}$/day and kg DM/head/day) offered to weaner stags during winter, spring and summer.*

Season	Genotype		Pasture Allowance			
Winter	Both	kg DM/$W^{0.75}$/day	0.10	0.13	0.19	0.25
	Red	kg DM/head/day	2.0	2.7	3.8	5.1
	Hybrid	kg DM/head/day	2.3	3.0	4.3	6.0
Spring	Both	kg DM/$W^{0.75}$/day	0.10	0.13	0.25	0.4
	Red	kg DM/head/day	2.3	3.8	5.7	9.1
	Hybrid	kg DM/head/day	2.8	4.3	6.4	10.3
Summer	Both	kg DM/$W^{0.75}$/day	0.16	0.23	0.29	0.45
	Red	kg DM/head/day	4.4	6.6	8.5	13.3
	Hybrid	kg DM/head/day	4.5	7.7	9.7	15.3

Higher feeding levels were achieved by increasing pasture allowance (kg DM/$W^{0.75}$/day) and pre-grazing pasture height (cm). This approach was necessary since it was impractical to confine deer to a small area on a high pasture mass (to achieve a low allowance) and there was insufficient grazing area to offer a large pasture allowance on a small pasture mass. Therefore, in this thesis, references to pasture allowance are associated with a specific pre-grazing pasture mass and references to increasing pasture allowance implies mass also increased.

No account was taken of concurrent pasture growth when calculating weekly grazing area.

The weekly grazing area for each treatment was calculated from Equation 1.

$$\text{Grazing area (ha)} = \frac{\text{Allowance (kg DM/W}^{0.75}\text{/day)} * 7 \text{ days} * \text{group mean metabolic lwt (W}^{0.75}\text{)} * \text{No. of deer}}{\text{Pre-grazing pasture mass (kg DM/ha)}} \quad (1)$$

Pasture measurement

Pasture height was measured in each treatment to the nearest centimetre using a lengthened copy of the HFRO sward stick (Hill Farming Research Organisation, 1986). Pasture height was defined as the greatest height above ground level that a leaf was in contact with the sward stick when placed perpendicular to the ground at a random site in the sward.

The mean pre- and post-grazing pasture height was estimated by measuring pasture height at 60 random sites per treatment.

Pre-and post-grazing pasture mass was estimated for each treatment from the mean pre- and post-grazing pasture height (as described above) and an allowance-specific relationship between pasture height and pasture mass which was updated weekly for each pasture.

The relationship between height and mass was determined by selecting four quadrats (0.2 m^2) (which covered the range of low to high pasture height relative to that pasture allowance), estimating average pasture height in each quadrat (40 measurements/quadrat) and harvesting the area for DM determination. Pasture in quadrats was cut to ground level using an electric shearing plant (Oster, USA Ltd). Harvested pasture was washed in warm water and dried at 70°C for 48 h before weighing. A linear relationship was fitted to pasture height and mass data and the resulting equation used to predict pasture mass from mean sward height in each weekly break.

Every alternate week the mean pasture height of each treatment was measured daily in order to describe the reduction in height during the week.

Botanical composition

A 10 x 20 cm area of pasture immediately adjacent to each pre-grazing quadrat cut was harvested to ground level using the method employed for the quadrat cut. This sample was frozen for later pasture botanical composition determination. Samples were thawed at room temperature, pooled so that one sample existed for each pasture allowance in each season, and a representative sample taken. Approximately 50 g of each bulked sample was dissected into grass leaf, grass pseudo-stem, clover, dead material, reproductive growth and weeds. Each dissected pasture component was placed in a paper bag and dried for 36 h at 75°C before weighing. Samples were allowed to cool and then weighed to the nearest milligram.

Pasture management

During summer, grazed pasture was mechanically topped to remove any remaining reproductive growth to maintain quality. Following topping, pastures were irrigated with approximately 75 mm of water.

Statistical analysis

Pre- and post-grazing pasture height and pasture mass for areas grazed by red and hybrid deer within each allowance were compared using a paired *t*-test. Liveweight gain was determined by linear regression of weekly liveweight over time for each individual animal and this value analysed using Generalised Linear Models as a 2 x 4 factorial design with two genotypes, and four nutritional levels within season.

Logistic functions were fitted to mean group liveweight gain and allowance data using Sigmaplot (Jandel Corporation) curve plotting software.

3.2 Results

Liveweight gain

Mean liveweight gain during winter was low (58 g/day) and not significantly different between genotypes (P> 0.05) (Table 3.2.) or pasture allowances.

Liveweight gain in spring (218 g/day) was on average about four times that achieved in winter (58 g/day) and hybrids gained 73 g/day (40%) on average more during spring than red deer (P>0.05).

There was no significant difference (P>0.05) in mean liveweight gain between genotypes in summer.

Table 3.2 *Mean initial liveweight and liveweight gain (LWG) of stags at each allowance during winter, spring and summer.*

Season		**Pasture allowance (kg DM/head/day)**			
Winter	Allowance (kg DM/W $^{0.75}$/day)	0.10	0.13	0.19	0.25
	Red initial liveweight (kg)	55.5 ± 1.1	54.3 ± 1.5	56.5 ± 0.8	56.1 ± 1.3
	Hybrid initial liveweight (kg)	63.5 ± 1.2	64.0 ± 1.4	66.6 ± 1.4	69.2 ± 1.0
	Red LWG (g/day)	35 ± 9	68 ± 22	49 ± 11	78 ± 13
	Hybrid LWG (g/day)	61 ± 20	86 ± 15	39 ± 11	56 ± 18
Spring	Allowance (kg DM/W $^{0.75}$/day)	0.10	0.13	0.25	0.40
	Red initial liveweight (kg)	62.2 ± 1.0	67.8 ± 1.1	69.7 ± 1.6	69.2 ± 1.6
	Hybrid initial liveweight (kg)	75.8 ± 1.3	79.8 ± 1.7	79.5 ± 1.8	80.3 ± 1.4
	Red LWG (g/day)	53 ± 15	211 ± 14	231 ± 14	232 ± 25
	Hybrid LWG (g/day)	191 ± 28	207 ± 17	300 ± 19	319 ± 22
Summer	Allowance (kg DM/W $^{0.75}$/day)	0.16	0.23	0.29	0.45
	Red initial liveweight (kg)	79.6 ± 2.9	87.1 ± 2.2	85.5 ± 3.2	86.3 ± 2.0
	Hybrid initial liveweight (kg)	94.8 ± 1.2	100.3 ± 3.0	101.9 ± 3.0	110.2 ± 2.0
	Red LWG (g/day)	122 ± 15	236 ± 18	170 ± 24	230 ± 15
	Hybrid LWG (g/day)	101 ± 32	245 ± 23	184 ± 20	296 ± 17

Pasture height and mass

Mean weekly pre- and post-grazing pasture height and mass for red and hybrid weaners at each pasture allowance are presented in Tables 3.3 and 3.4, respectively.

Table 3.3 *Mean (± SEM) pre- and post-grazing pasture height (cm) for red and hybrid weaner stags on four pasture allowances during winter, spring and summer.*

			Pasture Allowance ((kg DM/W $^{0.75}$/day)			
			0.10	**0.13**	**0.16**	**0.25**
Winter	Pre-grazing	Red	4.5 ± 0.1	10.5 ± 0.8	13.3 ± 1.4	17.3 ± 1.9
		Hybrid	4.7 ± 0.2	10.0 ± 0.6	14.6 ± 1.9	17.0 ±1.9
	Post-grazing	Red	1.7 ± 0.1	3.0 ± 0.4	3.7 ± 0.6*	7.7 ± 0.8
		Hybrid	1.8 ± 0.2	3.0 ± 0.4	4.7 ± 0.7*	7.9 ± 0.7
			Pasture Allowance ((kg DM/W $^{0.75}$/day)			
			0.10	**0.13**	**0.25**	**0.40**
Spring	Pre-grazing	Red	5.3 ± 0.3	13.6 ± 0.4*	18.3 ± 1.1*	21.7 ± 0.8
		Hybrid	5.2 ± 0.2	14.5 ± 0.5*	19.3 ± 0.9*	21.6 ± 1.1
	Post-grazing	Red	3.7 ± 0.4*	8.2 ± 0.6	13.3 ± 0.4*	18.1 ± 1.3
		Hybrid	2.2 ± 0.2*	8.9 ± 0.5	14.3 ± 0.6*	17.9 ± 1.4
			Pasture Allowance ((kg DM/W $^{0.75}$/day)			
			0.16	**0.23**	**0.29**	**0.45**
Summer	Pre-grazing	Red	5.1 ± 0.2	14.4±0.5	19.2±0.4	21.4±0.8
		Hybrid	5.0 ± 0.2	15.0±0.4	19.0±0.3	21.4±0.9
	Post-grazing	Red	2.8 ± 0.2	7.8±0.7	12.7±0.6	16.3±0.8
		Hybrid	2.6 ± 0.2	8.0±0.1	12.9±0.6	16.8±0.7

* Indicates mean weekly pasture height is significantly (P<0.05) different between genotype treatments

Table 3.4 *Mean (±SEM) weekly pre- and post-grazing pasture mass (kg DM/ha) for red and hybrid weaner stags on four pasture allowances during winter, spring and summer.*

			Pasture Allowance ((kg DM/W $^{0.75}$/day)			
			0.10	**0.13**	**0.16**	**0.25**
Winter	Pre-grazing	Red	1190 ± 40	2630 ± 210	2590 ± 260	3460 ± 430
		Hybrid	1270 ± 80	2560 ± 220	2870 ± 400	3440 ± 450
	Post-grazing	Red	634 ± 110	1293 ± 200	1750 ± 330	2420 ± 310
		Hybrid	690 ± 170	1140 ± 160	1810 ± 300	2880 ± 300
			Pasture Allowance ((kg DM/W $^{0.75}$/day)			
			0.10	**0.13**	**0.25**	**0.40**
Spring	Pre-grazing	Red	1750 ± 130	3460 ± 170	4280 ± 310	4640 ± 200
		Hybrid	1690 ± 110	3640 ± 170	4310 ± 280	4620 ± 210
	Post-grazing	Red	1480 ± 120*	2370 ± 250	3700 ± 230	4870 ± 190
		Hybrid	1170 ± 40*	2480 ± 210	3910 ± 140	4840 ± 210
			Pasture Allowance ((kg DM/W $^{0.75}$/day)			
			0.16	**0.23**	**0.29**	**0.45**
Summer	Pre-grazing	Red	1970 ± 120	3640 ± 170	5050 ± 240	5010 ± 260
		Hybrid	1960 ± 80	3760 ± 250	5010 ± 240	5010 ± 280
	Post-grazing	Red	1520 ± 140	2570 ± 180	4920 ± 140	5150 ± 220
		Hybrid	1510 ± 150	2640 ± 180	5000 ± 170	5250 ± 150

* Indicates mean pasture mass is significantly (p<0.05) different between genotype treatments

There was no significant difference (P>0.05) between genotypes in pre- or post grazing pasture height in winter or summer. In spring, there were significant differences (approximately 1 cm)

between hybrid and red pre- and/or post-grazing pasture height at an allowance of 0.25 and 0.13 kg DM/W$^{0.75}$/day (Table 3.4) but these did not equate to significantly different pasture masses. These data indicates that the aim of providing genotypes with equal opportunity in terms of pre-grazing pasture height and mass was largely achieved and any significant differences in pre-grazing height were small.

Pasture botanical composition

Composition of pasture offered varied with both season (spring and summer) and pasture mass (Table 3.5). Botanical samples were not collected in winter due to the wet ground conditions that prevailed.

Table 3.5. *Mean pasture mass (kg DM/ha) and botanical composition of pasture (% DM) at each allowance (kg DM/W $^{0.75}$/day) during spring and summer.*

	Spring					Summer			
Allowance (kg DM/W $^{0.75}$/day)	0.10	0.13	0.25	0.40		0.16	0.23	0.29	0.45
Pasture mass	1720	3550	4300	4630		1960	3700	5030	5010
Leaf	53.3	42.4	54.7	43.9		56.8	46.8	50.1	43.5
Pseudo-stem	19.2	12.7	12.4	15.2		8.5	1.9	.9	2.1
Clover	3.7	7.0	1.9	5.6		20.1	14.1	5.6	3.2
Dead material	19.0	13.2	17.4	13.0		11.8	19.1	25.1	20.3
Reproductive growth	2.9	20.5	9.0	17.1		2.5	8.7	14.5	14.5
Weeds	1.9	4.2	4.6	5.2		0.3	9.4	3.8	16.4

As pasture mass and allowance increased, the proportion of dead material, reproductive growth and weeds in the sward increased regardless of season, but grass leaf plus clover was always greater than 45% of total DM. The proportion of clover declined with increasing pasture mass during summer but not spring. The irrigation and topping regime was responsible for the relatively low proportion of reproductive components in the pasture during spring and summer. These data show genotypes were offered high quality spring-summer pasture.

Relationship between pasture allowance and liveweight gain

A three-term logistic function was fitted to spring and summer pasture and liveweight gain data (Figure 3.1). The function was;

$$LWG = a + b\,(1 - e^{(-c\,PA)})$$

Where liveweight gain (LWG) was expressed as g/day and pasture allowance (PA) as kg DM/kg $^{0.75}$/day. The term "a" represented the LWG when pasture allowance was zero, "b" the maximum liveweight gain and "c" the fractional slope of the curve from "a" to "b". The function, which assumes an asymptotic relationship, does not force the regression through the origin recognising that feed is required for maintenance before growth occurs. The coefficients for the equations are given in Table 3.6.

Alternative curvilinear functions such as the Mitcherlich used by Reid (1986) and Gibb and Treacher (1976) and the inverse linear as reviewed by Pringle and Wright (1981) for unpublished data cited in Hodgson (1984) explained similar amounts of variation in liveweight gain data.

An attempt was made to fit a linear relationship to winter liveweight gain due the lack of a curvilinear response. ($P>0.05$) (Fig 3.1a.). However, for both red and hybrid deer neither the intercept nor slope coefficients were significantly different from zero.

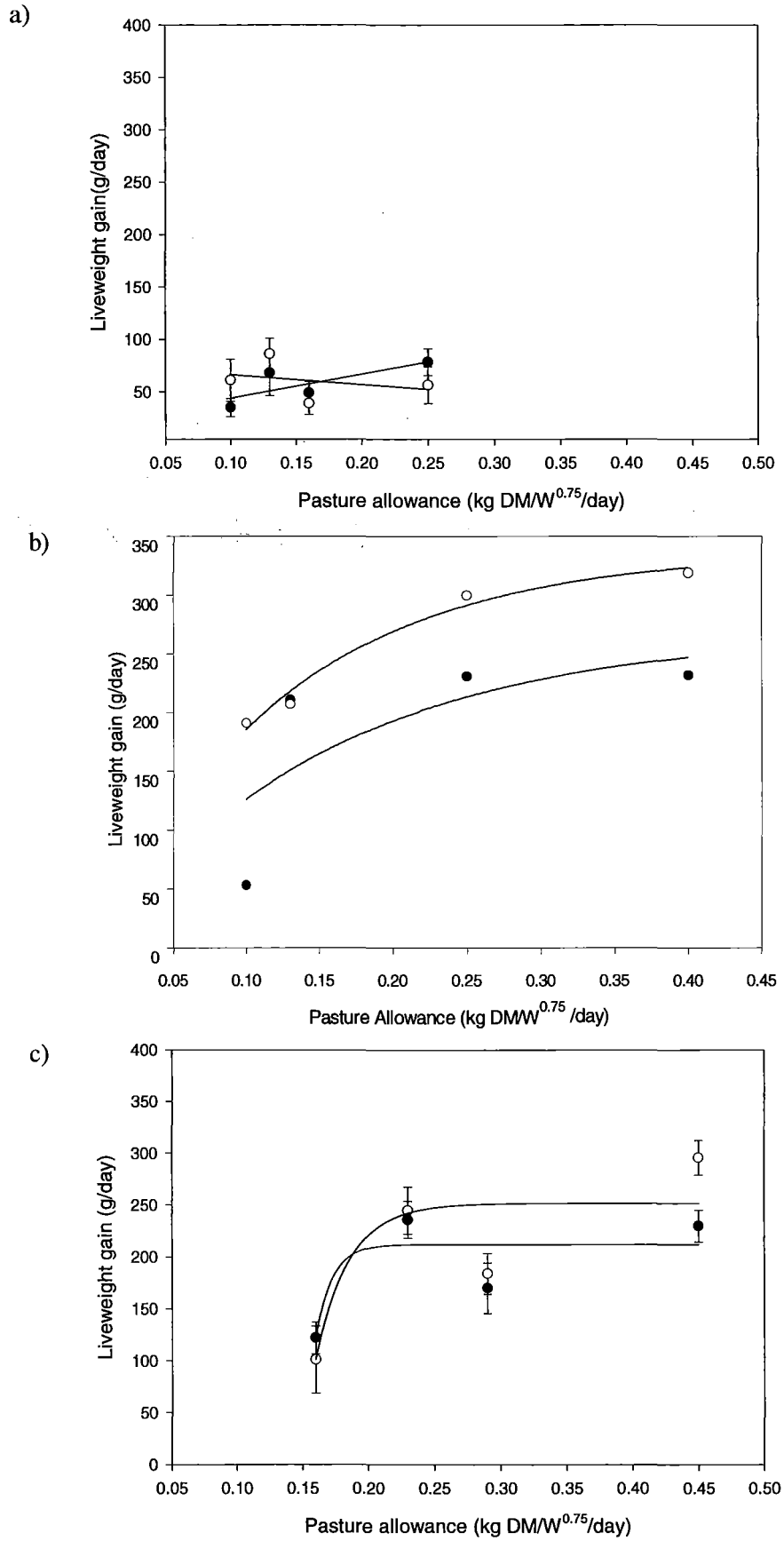
During spring, both genotypes responded to increases in pasture allowance, although in both spring and summer there was a decreasing marginal response to extra feed.

For red deer and hybrids during spring, liveweight gain plataeued at 307 g/day and 341 g/day, respectively. The corresponding values for summer were 225 and 255 g/day, respectively.

Table 3.6. *Fitted coefficients (see text above) for the logistic relationship between liveweight gain and pasture allowance.*

Season		a	b	c	R^2
Winter	Red		10.1	23.1	0.51
	Hybrid		-5.3	81.0	0.19
Spring	Red	-38.5	306.5	6.4	0.57
	Hybrid	-40.6	340.9	8.0	0.98
Summer	Red	-48.6	225.1	5.7	0.46
	Hybrid	79.1	255.3	3.9	0.48

Figure 3.1. *Liveweight gain of red (●) and hybrid (O) deer over a range of pasture availabilities during a)winter b)spring and c)summer. Error bars depict within-group SEM. Lines represent equation in Table 3.6.*



Partition of liveweight gain to pasture characteristics

Stepwise multiple regression was used in an attempt to partition the variance in liveweight gain to various components of pasture availability, pasture quality and animal factors. Pasture allowance variables such as pre-grazing height and mass, post-grazing height and mass, availability (product of pre-grazing mass and allowance), pasture quality variables which included green pasture mass, percentage of dead material and percentage of clover and fixed effects such as genotype and previous nutritional treatment(s) were added to a model to test if their inclusion significantly improved prediction of liveweight gain as indicated by a significant *t*-test ($P< 0.05$) for each variable.

Correlated variables

The correlation (Pearson's correlation coefficient) between the dependant variable liveweight gain and selected independent variables is presented in Table 3.7, and the correlation matrix between all variables for each season is given in Appendix I.

During winter, liveweight gain (absolute (g/day) and relative ($g/W^{0.75}$/day)) was only significantly correlated with initial weaner liveweight (-0.198). During spring, liveweight gain (absolute and relative) was most highly correlated with pre-grazing height (0.610), pre-grazing mass (0.602) and green pasture mass (0.602). Summer liveweight gain was most highly correlated with the per head allowance (0.543), pre-grazing height (0.575), and the percentage of grass leaf in the sward (-0.713).

All allowance-type variables such as per-head and relative allowance and pasture-type variables such as pre- and post-grazing mass and height were highly inter-correlated (0.8 - 1.0). This was a direct result of confounding pasture mass (and height) and allowance in trial design

All botanical parameters were highly correlated (0.85 - 1.0) with pre-grazing height and allowance and therefore would be unlikely to explain additional variation if added to a model which contained allowance type variables.

The relationship between liveweight gain and pasture and animal variables was only slightly stronger when liveweight was expressed as g/day rather than on a metabolic body weight basis ($g/kg^{0.75}$/day). Only predictions of absolute liveweight gain have been presented. A curvilinear function relating liveweight gain to pasture allowance accounted for only a marginally higher proportion of the variation than a linear function. The 1/allowance (inverse linear) and log (base 10) transformations gave similar results although the 1/allowance transformation was marginally better and therefore was used in the regression model. Pasture allowance was expressed as kg DM/head/day although, alternatively, allowance could have been expressed on a metabolic body weight basis with little effect on the final outcome.

Table 3.7. *Correlations (Pearson's correlation coefficient) between mean liveweight gain (g/day) and selected allowance, animal-related and pasture variates.*

Variable		Winter	Spring	Summer
Allowance variables	Allowance (kg DM/kg$^{0.75}$/day)	0.034	0.543	0.473
	Pre-grazing height (cm)	0.065	0.610	0.575
	Post-grazing height (cm)	0.068	0.570	0.539
	Availability	0.046	0.500	0.550
	Pre grazing mass (kg DM/ha)	0.123	0.602	0.505
Animal variables	Initial liveweight	-0.198	0.509	0.164
	Source of stock	0.153	0.054	0.085
	Parentage	-0.057	0.228	0.067
Pasture variables	Green pasture mass	-	0.602	0.385
	Leaf content	-	-0.172	-0.713
	Legume content	-	-0.008	-0.474
	Dead matter content	-	-0.353	0.374
	Pseudo-stem content	-	-0.455	-0.545
	Reproductive content	-	0.345	0.486

Pasture availability

The term pasture availability is used here specifically to define a concept which combines the effect of pasture allowance *per se* and the independent effect of pre-grazing pasture mass on animal response (Hodgson, 1981). Pasture allowance is defined as the mass of pasture offered to an animal over a given time but ignores the pre-grazing mass at which this is offered. Alternatively, liveweight gain is higher on higher pasture masses at a given pasture allowance (Rattray and Clark, 1984). A combination of the two approaches which described how *available* (pasture height and mass allocated to each animal) the pasture was to animals was investigated as a predictor of liveweight gain. Availability defined in this way explained less variation in liveweight gain than either pre-grazing height or allowance alone (Table 3.7).

Prediction of liveweight gain

During winter, neither pasture or animal variates accounted for significant proportions of variation in liveweight gain. This suggests the relatively small amount of variation in liveweight gain which existed at this time was of a random nature. Although a greater proportion of variation in liveweight gain could be explained in the spring and summer periods (53% and 33% respectively) compared with the winter a large proportion of the variation was unexplained and therefore the ability to explain liveweight gain was poor. The major problem faced by this type of analysis was the high inter-correlation between pasture variates and allowance, both of which would have been expected to explain a large proportion of the variation in liveweight gain as reported by Thompson (1992). Table 3.8 gives the coefficients and standard deviations of those factors and variates which significantly improved prediction of liveweight gain from pasture allowance or pre-grazing pasture mass alone.

Table 3.8. *Coefficients and standard errors for the regression of liveweight gain on 1/allowance or 1/pre-grazing height together with significant variates and factors.*

Winter	Constant	Liveweight	Genotype	Pre-Mass		R^2
	150 ± 51	-1.5 ±0.8				2.6
	236± 60	-3.9± 1.2	49 ±16			7.3
	234 ±59	-4.6± 1.3	47± 16	0.10 ± 0.01		13.1
Spring	**Constant**	**1/per-head**	**Genotype**	**Parentage**	**Liveweight**	**R^2**
	320 ±16	-400± 54				36.3
	211 ±26	-40± 49	72 ±15			49.1
	242 ±31	-426 ±51	48± 20	0.95 ±.52		50.4
	101± 97	-389± 55	25± 25	0.84± .53	2.3 ±1.5	51.1
Summer	**Constant**	**Leaf content**	**Clover content**	**1/per-head**		**R^2**
	783± 66	-11.8 ±1.3				48.6
	868 ±89	-14.1± 2.0	2.1 ±1.5			50.2
	750 ±142	-10.4 ±4.0	6.2± 4.2	-783± 736		51.0

where;
1/per - head = reciprocal of allowance per head
Leaf content = percentage of leaf in sward
Leaf content = percentage of leaf in sward
Clover content = percentage of clover in the sward
Liveweight = initial liveweight (kg) for each season
Parentage = genotype determined by blood typing, expressed as the proportion of elk genes

Compensatory growth

This experiment was not specifically designed for the purpose of investigating compensatory growth in deer. However the opportunity was taken to compare the liveweight gain of deer from different previous treatments during the 7-week post-experimental periods. The relationship between mean liveweight gain of treatment groups during and after experimental periods is given in Figure 3.2.

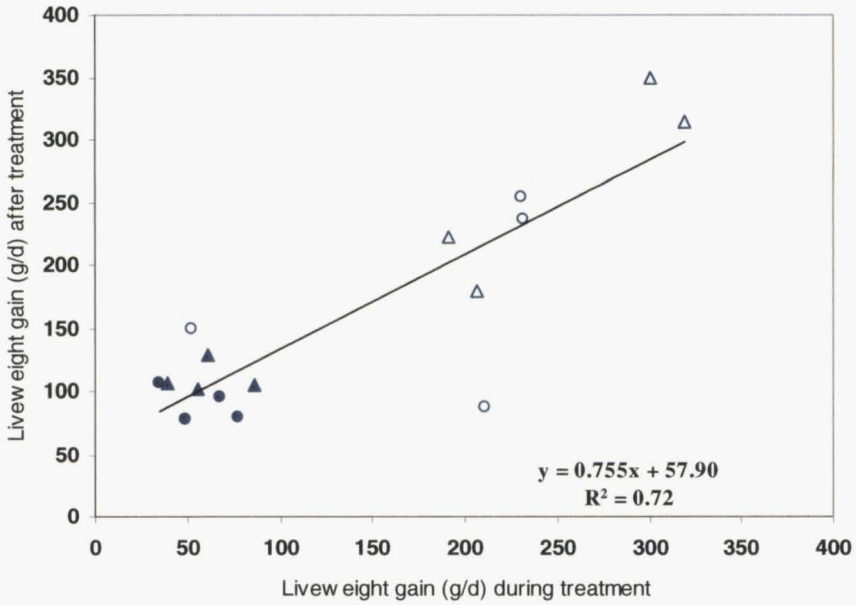


Figure 3.2. *Mean liveweight gain (g/day) of groups of red (O) and hybrid (Δ) deer during and after winter (solid) (n=12/group) and spring (open) (n=10/group) experimental periods for each pasture allowance treatment.*

Mean group liveweight gain during winter treatments ranged between 35 and 86 g/day. The regression coefficient for the relationship between treatment and post-treatment liveweight gain was not significantly different from zero and on average weaners gained liveweight at 109 g/day post-treatment.

During the spring experimental period mean group liveweight gain ranged from 53 to 319 g/day. For every additional 100 g/day liveweight gain during experimental treatment, post-treatment liveweight gain increased by 74 g/day.

The relationship between treatment and post-treatment liveweight did not differ between red and hybrid deer or for spring and spring/winter combined.

Liveweight model and prediction of time of sale

Initial liveweight (1 June) and liveweight gain measured during winter and spring were used to simulate liveweight of deer at 12 months of age for both genotypes based on the allowances offered in both winter and spring (Table 3.9). The expected liveweight at 12 months was calculated for each allowance as;

12 month wt (kg) = 1 June wt (kg) + (winter LWG (g/day) x 75-day winter) + (spring LWG (g/day) x 121-day spring)

where winter/spring LWG was the average liveweight gain recorded during the winter/spring for deer on each allowance and the winter period was the 75 days from 1 June - 15 August and the spring period the 121 days from 16 August - 15 December. The simulated mean 12 month weight and the measured standard deviation of liveweight in treatment groups at 12 months was used to estimate the percentage of animals in each group which would have attained 92 kg liveweight by 15 December assuming deer liveweight was normally distributed.

On this basis, less than 30% of red deer reached target liveweight at any allowance, compared with 68 - 99% of hybrids reaching this slaughter target by 15 December depending on allowance offered. Even at high allowances, 60% of the difference between genotypes in liveweight at 12 months existed in 1 June weight. This proportion was greater at lower allowances.

Table 3.9. *Winter liveweight (measured), 12 month liveweight (simulated) and the percentage of animals attaining 92 kg liveweight for red deer (Red) and hybrids (Hyb) over a range of pasture allowances . The percentage of the difference in 12 month weight between the genotypes which existed in 1 June weight is also given (spring:winter genotype difference).*

Allowance kg DM/W $^{0.75}$/day	0.10		0.13		0.19 winter 0.25 spring		0.25 winter 0.40 spring	
Genotype	Red	Hyb	Red	Hyb	Red	Hyb	Red	Hyb
Mean 1 June wt (kg)	57.7	68.5	57.7	68.0	57.4	67.6	57.0	67.8
Mean 12 month wt (kg)	82.3	94.8	83.3	96.4	85.0	99.5	87.2	104.8
Standard deviation (kg)	3.9	8.0	5.5	5.3	7.3	8.7	7.8	7.6
Percent reaching 92 kg	1	64	6	80	17	81	27	95
Spring:winter genotype difference	87		80		70		61	

Liveweight gain per hectare

The number of deer reaching a 92 kg target is a measure of per head performance within a production system but it gives no information on the per hectare performance. The rate of liveweight gain and stocking rate of deer at each allowance was used to calculate liveweight gain per hectare during spring and summer (Table 3.10). Liveweight gain per hectare (kg/ha/week) was calculated as;

$$\text{LWG kg/ha/week} = \text{LWG (g/day)}/1000 \times 7\text{days} \times \text{stocking rate (deer/ha)}$$

where LWG was the mean liveweight gain of each treatment group for spring and summer respectively and stocking rate was the number of deer in each treatment group divided by the total area (ha) used in each grazing rotation.

Table 3.10. *The stocking rate (deer/ha), liveweight gain (g/day) and liveweight gain per hectare (g/ha/day) for red and hybrid deer in spring and summer for each pasture allowance.*

Spring								
Allowance kg DM/W $^{0.75}$/day	0.10		0.13		0.25		0.40	
Genotype	Red	Hybrid	Red	Hybrid	Red	Hybrid	Red	Hybrid
LWG (g/day)	53	187	211	207	231	305	232	319
Stocking rate(deer/ha)	26.8	22.9	23.7	21.6	15.3	14.0	7.8	7.1
LWG/ha (kg/ha/week)	10	30	35	31	25	30	13	16
Summer								
Allowance kg DM/W $^{0.75}$/day	0.16		0.23		0.29		0.45	
Genotype	Red	Hybrid	Red	Hybrid	Red	Hybrid	Red	Hybrid
LWG (g/day)	122	93	233	245	170	184	230	297
Stocking rate(deer/ha)	18.2	16.1	15.8	14.9	11.5	10.4	6.0	5.2
LWG/ha (kg/ha/week)	16	10	26	26	14	13	10	11

During spring, the greatest liveweight gain per hectare for both genotypes occurred at an allowance of 0.13 kg DM/W $^{0.75}$/day. At this allowance red deer produced an extra 4 kg of liveweight per hectare compared with hybrids.

However, while hybrids produced less liveweight per hectare at an allowance of 0.13 kg DM/W $^{0.75}$/day compared with red deer, the penalty to per hectare production of offering high allowances occurred at a lower allowance for red deer compared with hybrids. For example, increasing the allowance from 0.13 to 0.25 kg DM/W $^{0.75}$/day reduced liveweight gain per hectare by 10 kg/ha/week for red deer but had little effect on hybrids.

During summer, the greatest liveweight gain per hectare for both genotypes occurred at an allowance of 0.23 kg DM/W $^{0.75}$/day. Increases in allowance above this reduced per hectare liveweight gain

equally for both genotypes. Maximum liveweight per hectare occurred at about 80% of maximum liveweight gain per head. Maximising hybrid liveweight gain in spring halved per hectare production. Offering generous pasture allowances to red deer achieved the same outcome in terms of liveweight gain per hectare as offering low pasture allowances.

3.3 Discussion

This study generated novel liveweight gain-pasture allowance relationships for young deer grazing ryegrass-white clover pastures and provided a direct comparison of red and red-elk hybrid genotypes. In general, the liveweight gain responses to changes in pasture allowance were similar (Figure 3.1) but there was some suggestion (in spring) that (a) hybrids needed a greater allowance to maximise liveweight gain and (b) liveweight gain in hybrids may be more sensitive to low pasture allowance than in red deer.

Winter liveweight gain

Weaner stags in this study followed the general pattern of seasonal liveweight gain described in previous work (Kay, 1985; Semiadi, *et al.,* 1992; Ataja *et al.,* 1992; Kusmartono *et al.,* 1995) with low winter and high spring liveweight gain. The winter liveweight gain reported here (35 -85 g/day) was lower than that reported previously (140 - 165 g/day, Ataja *et al.,* 1992; 171 g/day, Kusmartono *et al.,* 1995) but similar to those reported by Semiadi *et al.* (1992) (106 g/day) and Soetrisno *et al.* (1994) (94 g/day) when compared at similar pasture allowances.

Differences in winter liveweight gain between this and other studies may have been either a function of which months were defined as winter, or a consequence of the wet conditions which prevailed during winter (see below). High winter liveweight gain has been reported by various authors who have included data collected in September in winter measurements. Deer housed over the early spring period showed an increase in DM intake and liveweight gain of 10% per week from mid-August (P.Fennessy *pers com*). When August data were removed from winter liveweight gain reported by Ataja *et al.* (1992), average liveweight gain of weaners decreased from 140 and 150 g/day to 50 and 60 g/day for deer grazing perennial and annual ryegrass, respectively. A further possible explanation of the relatively low winter liveweight gain in the present work is the high rainfall experienced during the winter period. During the 9 week winter experimental period 141 mm of rain fell and the prevailing wet underfoot conditions and readily muddied pasture may have lead to a reduction in intake and consequently a reduction in liveweight gain.

During winter, the response in liveweight gain to additional pasture was low. At best, increasing allowance increased liveweight gain for red deer from 35 to 78 g/day. Although no attempt was made to measure pasture utilisation, wastage through trampling, especially for high pasture allowances treatments, was likely to have been considerable. This suggests that in this environment there was no benefit to liveweight gain and probably considerable disadvantages in terms of utilisation in offering weaners large quantities of pasture during winter. The practice of shifting weaners on a weekly basis to offer them a low mass of "freshened" pasture in winter would now appear to have some scientific basis.

Deer grazed to a lower post-grazing pasture height at similar allowances during winter compared with spring and summer (Table 3.3.) which arguably may have been the cause of the lower liveweight gain during winter compared with spring and summer. However, it is questionable, considering the small response in liveweight gain to increasing winter post-grazing height, whether grazing to a winter post-grazing pasture mass equivalent to spring/summer values, would have significantly increased winter growth rate. For example, deer offered a winter pasture allowance of around 0.19 kg DM/$W^{0.75}$/day reduced a 13 cm high pasture to 4 cm and incurred a liveweight gain of 50 g/day. In spring, the same allowance was grazed to 8 cm and therefore would have been expected to reduce intake (Rattray and Clark, 1984). However, on the highest winter pasture allowance (0.25 kg DM/$W^{0.75}$/day) where pasture was reduced from 17 cm to 8 cm, liveweight gain was similar to that obtained on the lower pasture allowance, therefore the lower winter residual appears to have had little effect on liveweight gain.

Spring

Spring daily liveweight gain of both genotypes was high relative to winter (2.5 - 4 times) and similar to that reported previously (Ataja *et al.,* 1990; Semiadi *et al.,1*992; Kusmartono *et al.,* 1995) when compared at similar post-grazing pasture mass or pasture allowance. There was a large increase in liveweight gain in response to increasing pasture allowance from 1.8 - 3.7 kg DM/h/day but the increase above 3.7 kg DM/head/day for red deer was low (>20 g/day between allowance 3.7 and 9.1 kg DM/head/day) suggesting red deer were nearing their maximum intake at this allowance. When red deer were continuously stocked during spring, increasing sward height from 4 to 10 cm had no effect on liveweight gain (Hamilton *et al.,* 1995). In the present study, increasing pre-grazing pasture height from 5.2 to 13 cm increased spring liveweight gain of red deer from 50 to 200 g/day.

Hybrids continued to show a response to extra pasture allowance during spring (Figure 3.1b) even when allowance was high (6.4 kg DM/head/day) implying, unlike red deer, maximum intake had not been achieved. Extrapolation of the allowance curve (Figure 3.1b) suggests that an allowance of 10.3 kg DM/head/day may have supported near maximum intakes. For example, at an allowance of 10.3 kg DM/head/day hybrids gained liveweight at 323 g/day. The predicted liveweight gain from the fitted relationship for an allowance of 12.8 kg DM/head/day was 330 g/day.
These data indicates hybrids need to be offered almost twice the amount of pasture (5.7 vs 10.3 kg DM/head/day) as red deer during the spring to maximise liveweight gain.

At the lowest spring pasture allowance (0.16 kg DM/$W^{0.75}$/day), hybrid liveweight gain was 4 times that of red deer but it seems that hybrids were prepared to graze lower into the sward to maintain intake when feed supply was limited during spring (Table 3.3). That is, a pasture allowance intake relationship at the lowest spring pasture allowance may have been different for hybrids compared

with red deer. It is possible that such an effect could also have been responsible for a genotype difference in liveweight gain at higher allowances, although no difference in the residual grazing height of pastures between genotypes was detected at the higher allowances However, the methods of height measurement employed in this study were not sufficiently sensitive to pick up the relative small differences needed. For example, at the highest allowance pasture height was reduced on average by 4 cm during grazing by either genotype. Since the standard error of the mean for the height measurement at the highest allowance was 1.3 cm it is likely any subtle differences in post-grazing pasture mass would not have been detected. A difference in post-grazing pasture mass of 1.3 cm is equivalent to a 0.55 kg DM/day or a 20% increase in intake per animal. So, although hybrids have been shown to gain liveweight faster than red deer during spring even although they grazed to an apparently similar residual, it is still possible that a difference in DM intake was responsible for the difference in liveweight gain.

There is evidence that animals which possess a high potential for production have a higher intake than less productive animals and under feed restrictions are prepared to work harder to obtain it. Studies on dairy cows has shown that pen-fed Friesians produce up to 50% more total milk than their Jersey counterparts, but require 20% more feed (Blake *et al.*, 1986; Gibson, 1986). Friesians, a high producing large genotype, graze to a lower post-grazing pasture mass (L'Huillier *et al.*, 1988) compared with Jersey cows. Within the Jersey breed, Bryant (1983) found cows of high genetic merit grazed to a lower residual when restricted than cows of lower genetic merit. Similarly, genetically superior Friesians ate more DM/100 kg liveweight than their genetically inferior contemporaries, and the effect was greatest when allowances were high. This concept may explain the lower post-grazing pasture mass recorded for hybrid deer at low allowances during spring in this study.

Summer

Mean summer daily liveweight gain was similar for both genotypes, due mainly to a reduction in liveweight gain of hybrids compared with spring, rather than any increase in red deer liveweight gain from spring to summer. Previous studies of this kind have slaughtered stags at, or before, December and therefore comparable literature for summer is scarce. The liveweight gain response to changing allowance was similar for both genotypes and allowances above 6 kg DM/head/day produced little extra liveweight gain. The similarity in botanical composition of the spring and summer swards (Table 3.5) indicated removal of reproductive growth and the use of irrigation enabled pasture quality to be maintained at a time when, under normal pasture management, quality would have declined. This suggests that the reduction in liveweight gain observed during the summer was an animal effect rather than an effect caused by a changing quality of diet, although it is likely that further reduction in liveweight gain would occur in situations where high pasture quality was unable to be maintained.

Prediction of liveweight gain

Multiple regression equations which used pasture and animal variates as factors to predict liveweight gain were unable to explain as high a proportion of variation in deer liveweight gain as that recorded in other studies with other species (Thompson, 1992). A major difference between this and many other pasture allowance type experiments was the confounding of pasture allowance with pre-grazing pasture mass and height. Consequently, this work was not effective at isolating effects of components of pasture availability on intake and liveweight gain although this was never the intent, which was to compare genotypes over a range of pasture availabilities. However it invites the question as to whether hybrids responded more to extra pasture height or extra allowance.

The regression coefficient for allowance in the multiple regression of the current study was higher than those previously published. This was not surprising considering pasture allowance was highly and positively correlated with pasture mass. Figure 3.3 presents the fitted curves for these data and a series of hypothetical pre-grazing pasture mass curves (Rattray and Clark, 1984). It suggests that increasing both pasture allowance and pasture mass produced a response curve which transects a number of pasture mass specific allowance-liveweight gain relationships and therefore the increase in liveweight gain was in some cases much greater than has previously been reported.

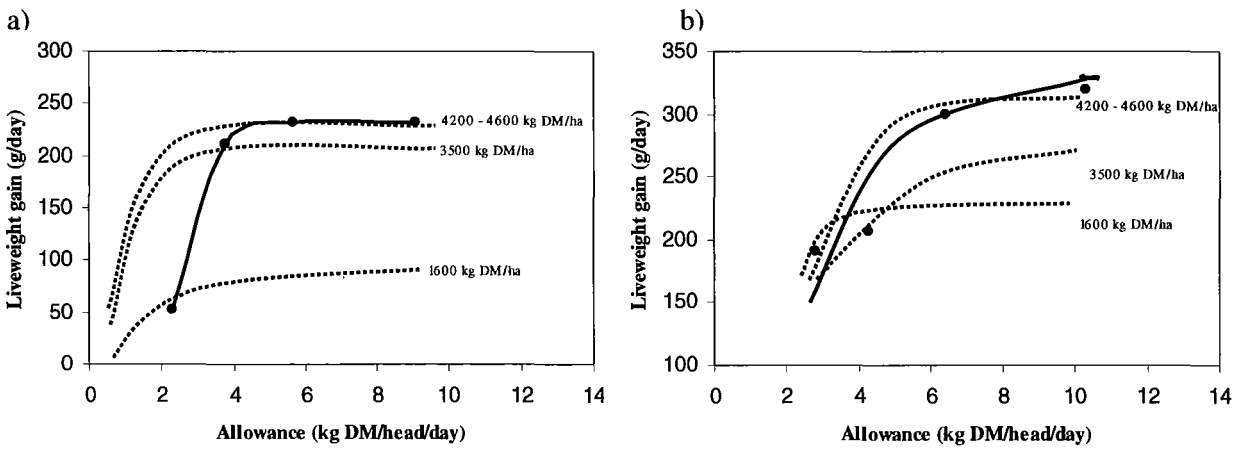


Figure 3.3 *The mean allowance-liveweight gain relationship for red (a) and hybrid (b) deer during the spring over a range of pasture masses (solid line) and hypothesised range of pasture allowance-liveweight gain relationships at common pasture masses.*

Experimental approach

The lack of replication in the trial design and the confounding of pre-grazing pasture mass and daily allowance reflect design limitations but were the practical realities of this research.

A replicated design would have enabled a more rigorous analysis of pasture allowance effects on liveweight gain by allowing for analysis by ANOVA of group means rather than individual animal values. However, replication would have involved many more resources than were available. While

ANOVA techniques have been used in the analysis of these data to identify deer genotype effects, the author acknowledges the tentative nature of results from this work.

Further, the experimental treatments were complicated by confounding daily pasture allowance and pre-grazing pasture mass, both known to independently influence intake and liveweight gain (Hodgson, 1982). However, in an experiment where the primary aim was to compare deer genotype over a range of feeding levels, it is more important to ensure groups within feeding treatment had similar nutritional opportunities rather than to define exactly the feed treatments. This experiment measured pasture allowances without including concurrent pasture growth. Thus differences in the pasture available for grazing between allowance treatments may have been greater than that represented purely by allowance and errors in pre-grazing height and mass would have lead to errors in the calculation of allowances.

Confounding made it impossible to clearly identify whether weaner stags responded more to increases in pasture height and mass or pasture allowance but Figure 3.3 suggests allowance was important. However, these data have practical application because the greater pasture mass at which high allowances were offered probably reflects on-farm situations more realistically than a range of allowances at a common pasture mass.

Effect of liveweight gain on 12 month weight

In previous studies investigating venison production in New Zealand, the proportion of deer attaining 92 kg by 12 months of age has been used to evaluate nutritional, management and genotype treatments. Over recent years this target has been increased to 95 kg but to allow a comparison with previous years a target of 92 kg will be used. Based on simulated data, a pasture system run at the highest allowance would only achieve 92 kg liveweight in 27% of red deer. This is similar to farm survey data (Wilson and Audige, 1996) which indicates an industry average of about 10-15% of red deer reach 92 kg within 12 months. These proportions are low compared with 75% reported by Semiadi *et al.* (1993a), 90% by Soetrisno *et al.* (1994) and 100% by Kusmartono *et al.* (1995) who all offered allowances less than the highest allowance in the present study. The difference between studies appears to be more due to greater initial liveweight than liveweight gain. If pre-winter liveweight of 62 kg as reported by Semiadi *et al.* (1993a), is used as the initial weight in the simulation (instead of 58 kg), 56% of red deer would have reached 92 kg by December which is more comparable with previous studies. The proportion of hybrids reaching 92 kg from the highest pasture allowance (99%) was similar to that reported by Kusmartono *et al.* (1995) who fed at a similar level and recorded a similar pre-winter liveweight to the present study. Increasing hybrid pre-winter liveweight by 4 kg would have enabled all hybrids to reach 92 kg in 12 months on a lower (6 vs 10 kg DM/h/day) pasture allowance than offered here.

Therefore the higher 12 month liveweight of hybrids compared with red deer is a combination of their more rapid liveweight gain in spring (9-10 months old) and greater pre-weaning (autumn) liveweight. In this study, spring liveweight gain only accounted for, on average, 26% of the difference in 12 month liveweight with the majority of the liveweight difference (74%) existing at the beginning of winter (Table 3.4). To illustrate the extent to which weaning weight (1 March) and liveweight gain interact, the percentage of deer reaching 92 kg liveweight by mid December for given combinations of weaning weight and average liveweight gain was calculated (Figure 3.4). Similar tables for liveweight in November and October are given in Appendix II.

Average LWG (g/day) (1 March to 15 Dec)

March liveweight (kg)	100	125	150	175	200	225
	percentage of animals reaching 92 kg					
40	0	0	0	7	47	90
45	0	0	4	35	84	99
50	0	2	24	75	98	100
55	1	16	64	96	100	100
60	9	52	92	100	100	100
65	40	87	99	100	100	100
70	57	92	100	100	100	100

Figure 3.4. *Effect of weaning weight (1 March) and liveweight gain on the percentage of deer reaching 92 kg liveweight by mid December. Stippled and shaded areas represent likely scenarios for red and hybrid deer, respectively.*

With a mean weaning weight of 50 kg (industry average for red deer) only average growth rates of above 200 g/day allow significant numbers of deer to reach 92 kg by the target date. Such average growth rates are seldom achievable by red deer (Wilson and Audige, 1996). In contrast, most hybrids with an average weaning liveweight of 60 kg will achieve 92 kg liveweight mid-December, even with a low liveweight gain (125 g/day). In this experiment red deer grew on average between 125 and 150 g/day for the lowest and highest pasture allowance, respectively. For hybrids, the corresponding figures were 135 and 200 g/day. Weaning weights were 50 and 58 kg for red deer and hybrids, respectively.

Liveweight gain per hectare

Where high pasture allowances were offered during spring (10 kg DM/head/day), deer gained liveweight rapidly (230 - 320 g/day for red deer and hybrids, respectively) but did so at the cost of per hectare liveweight gain. In this experiment the greatest liveweight gain per-hectare was achieved on a pasture allowance of about 4 kg DM/head/day. At this allowance red deer achieved both a high liveweight gain per head and per hectare but the greatest production per hectare from hybrids occurred well below the maximum per head production. This suggests that previous studies which have used liveweight gain per head as their only criteria for measuring the success of grazing systems (Ataja *et al.*, 1992; Semiadi *et al.*, 1993a; Soetrisno *et al.*, 1994; Kusmartono *et al.*, 1995) may not have identified the most productive system for hybrids on a per hectare basis.

Compensatory growth

In the period after experimental treatment, deer did not exhibit compensatory growth as a result of the feed restriction imposed previously. In other studies involving the release to spring pasture of feed-restricted deer housed during winter, the lack of compensatory liveweight gain was attributed to the low pasture mass offered (1000 kg DM/ha) during the opportunity for compensation (Loudon and Milne, 1985). Red deer, restricted during winter did show an extra 37 g/day extra growth compared with *ad lib.* fed animals when released onto pasture of mass no less than 1500 kg DM/ha in the second year of a trial, although during the first year under similar conditions no compensation was evident (Webster *et al.*, 1997). A similar study showed housed red deer grew at 241 and 138 g/day during winter for a high and low plane of nutrition respectively and grew at 137 and 176 g/day respectively when released to pasture during spring (Brelurut *et al.*, 1995). Although there is no information on compensatory growth in hybrids, Wairimu *et al.* (1992) found that after long restrictions during winter, wapiti stags grew faster (350 g/day) than their *ad lib.* fed counterparts (160 g/day) when both were supplemented with hay on spring pasture.

While there was no measurement in the present study of the pasture mass offered to deer in the period between experiments, during winter, it would have been less than that offered by Loudon and Milne (1985). After spring treatments, deer were offered almost certainly more than 1500 kg DM/ha, on pasture which had neither been topped or regularly irrigated and consequently would have been substantially poorer in quality compared with experimental pastures. It is possible therefore that, as hypothesised by Loudon and Milne (1985), deer in the present study were not given the pasture mass (winter) or pasture quality (summer) to allow them to exhibit any compensatory growth. However, given the pasture supply offered in summer was able to sustain liveweight gains in excess of 250 g/day in some individuals, it is unlikely that quality or quantity was a major factor limiting the ability for deer to compensate.

Severity and duration of feed restriction is known to affect the degree of compensation (Wilson and Osbourn, 1960). Although liveweight gain during winter was low it was similar across all allowances and consequently there was no significant difference in liveweight between treatment groups. Therefore, compensation would not be expected.

However, the same could not be said for deer during the period post-spring where previous restriction in feed intake had a large effect on liveweight gain. The difference in liveweight between deer on the highest and lowest allowances at the conclusion of the spring experiment was 16.7 and 12.8 kg for red deer and hybrids respectively. It would appear that the severity of restriction should have been sufficient to initiate compensatory growth since previous experiments where restriction has been responsible for 19.6 kg (Brelurut *et al.*, 1995) and 12.4 kg (Webster *et al.*, 1997) differences, compensatory growth has been recorded.

Some previous authors (for example, Carston *et al.,* 1991; Wairimu and Hudson, 1993) attributed some of the increased liveweight gain after restriction to an increase in gut fill although Yambayamba *et al.* (1996) found no difference in gut fill between restricted and non-restricted animals. If increases in gut fill were associated with compensatory gain in the current experiment, where there appeared to be little difference in liveweight gain post-restriction between restricted deer and those on high pasture allowances, subtracting a gut fill effect from restricted animals further increases the apparent body weight gain of well fed deer compared with their restricted cohorts.

This work suggests that liveweight gain sacrificed due to feed restrictions during spring is irretrievable as it appears that deer are unable to compensate later in the season. However, more work specifically focusing on this is needed.

3.4 Conclusions

This study shows that hybrids have a greater liveweight gain at any pasture allowance compared with red deer in spring but that differences during winter and summer are not significant. This finding is consistent with farm based observations that when feed is restricted, the hybrid is unable to exhibit its superior potential for liveweight gain over red deer. At the lowest spring pasture allowance hybrids grazed to a lower residual compared with red deer, and consequently had a greater apparent intake, but it is unclear, due to the inability to measure accurately high pasture masses with the techniques employed, whether genotype differences in intake were responsible for the liveweight gain differences observed at higher pasture allowances. What is clear is the greater potential of hybrids to achieve high liveweight gain compared with red deer in spring, but with the need to offer hybrids almost three times the pasture allowance required by red deer to reach their potential.

Chapter 4a

Effect of season on feed intake and liveweight gain of group – fed young red deer (*Cervus elaphus)* and red x elk hybrid stags

4.0 Introduction

In the experiment described in Chapter 3 marked differences existed between genotypes in the seasonal pattern of liveweight gain at high pasture allowances (presumably close to *ad lib.* intake). In red deer, it has been shown previously that seasonal patterns in liveweight gain reflect seasonality of feed intake (Loudon, 1994; Webster, 2000). It is possible that differences between genotypes in amplitude of liveweight gain between winter and spring observed in Experiment 1 reflect a different seasonal pattern of intake between genotypes.

Alternatively, there is good evidence that the energy requirement for maintenance of deer differ between winter and summer and some evidence the winter-summer amplitude may be higher for elk than for red deer (Simpson *et al.*, 1978a; Jiang and Hudson, 1994).

Although red deer and hybrids could differ in liveweight gain as a result of a number of other reasons, as demonstrated in the literature review (Chapter 2), the two experiments reported in Chapter 4a and 4b primarily focus on intake and maintenance requirement.

The experiment in Chapter 4a aimed to compare the relationship between *ad lib.* feed intake and liveweight gain of red and hybrid deer either to confirm that seasonal changes in the amplitude of liveweight gain reflect seasonal changes in *ad lib.* intake or, alternatively, to suggest a difference in maintenance requirement, or that some other effect such as composition or efficiency of gain may be involved in the seasonal genotype differences in liveweight gain.

In the previous experiment (Chapter 3) the largest difference in spring liveweight gain between red and hybrid weaners occurred at the highest pasture allowance, so in this experiment genotypes were compared only at *ad lib.* intake.

4.2 Materials and Methods

Experimental design

Total group *ad lib.* feed intake of a pelleted diet and individual liveweight gain were measured for housed red and hybrid weaner stags (approximately 6 - 12 months of age) in winter and spring.

Animals

Fifteen red weaner stags weighing 53.9 kg ± 1.3 kg (mean liveweight ± SEM) and fifteen red elk hybrid weaner stags weighing 62.3 kg ± 1.5 kg (mean liveweight ± SEM) were housed in two genotype-specific groups. Daily feed intake (per group) and liveweight gain (individual animal) were recorded for deer during 56 days in winter (3 July - 27 August) and 63 days in spring (16 October - 16 December). Deer were housed for 2 weeks under experimental conditions prior to data collection. Stags were housed at a density of 1 animal per 3.9 m^2 (Plate 4.1).

Red deer were sourced from 2 commercial herds from the Canterbury area and the hybrids from a third. All deer received anthelmintic (1 mg /10 kg liveweight, Vetdectin, Cyanamid NZ Ltd) and copper (5 g copper oxide needle containing bolus, Copacaps, Rhone Merieux) prior to housing in both seasons.

Deer were weighed weekly, before feeding, in a deer crush mounted on load bars (Tru-test, model 700 economy plus, Tru-test Distributors Ltd, Auckland). Mean liveweight gain for individual deer was taken as the regression coefficient of the linear relationship between liveweight (kg) and time (days) and expressed as grams per day.

Plate 4.1. *Single genotype groups of red and hybrid deer housed and offered a pelleted diet ad lib.*

Feeding

Deer were offered feed daily at 0900 h. The ingredients and proximate analysis of the pelleted ration offered are given in Table 4.1. The feed offered daily to each group was increased if the feed refused from the previous day (residuals) for that group was less than 10% of the feed on offer. Residual feed was collected daily, weighed and discarded.

Table 4.1. *Raw ingredients and proximate analysis (DM basis) of winter and spring batches of a barley-based concentrate feed*[1].

Raw ingredients	**g/kg DM**	
barley grain	468	
bran/Pollard	460	
mollasses	8	
$CaCO_3$	30	
NaCl/selenium premix	34	
Proximate anlaysis	**Winter**	**Spring**
dry matter (g/kg fresh)	912	881
organic matter (g/kg DM)	938	930
crude protein (g/kg DM)	142	147
fat (g/kg DM)	31	33
acid digestible fibre (g/kg DM)	96	100
dry matter digestibility (%)	88.8	87.6
organic matter digestibility (%)	90.2	90.7
M/D (MJ ME/kg DM)[2]	12.0	11.9

1. All-purpose ration (APR plus) Target Stock Feed, Archers Milling Company, Rangiora, NZ.
2. Calculated from the equation for compound feedstuffs (AACR, 1990).

Determination of feed intake

Daily feed intake was calculated for each group as;

Daily group intake (kg DM) = fresh feed offered (kg) x DM% - feed refused (kg) x DM%

Dry matter percentage (DM%) of offered and refused feed was determined daily over a 3 week period and the mean values used to calculate DM intake. To determine DM%, a sample of approximately 1 kg was weighed to the nearest 0.1 g, oven dried at 70° C for 36 h and re-weighed. Deer had unlimited access to water at all times. To prevent lengthy storage of the pelleted ration, a new batch of the same recipe was made prior to the beginning of each experimental period. Daily individual intake (kg DM/head/day) was calculated by dividing daily group intake by 15 (deer/group). ME intake (MJME /day) was calculated as M/D (MJME/kg DM) x DMI (kg DM/day).

Statistical analysis

Mean daily intake of red and hybrid weaner was analysed by comparing the group intake (on 56 days - winter or 63 days - spring) during the experiment using a students *t* test.

Liveweight gain was determined by linear regression of weekly liveweight over time for each individual animal. Red and hybrid groups were analysed by comparing liveweight gain of individual deer (n = 15) using a *t* test.

4.3 Results

Intake and liveweight gain

Ad lib. intake and liveweight gain during winter and spring of both genotypes are given in Table 4.2 with a table showing absolute values in Appendix 3. During winter, hybrids consumed more feed (115 g DM/head/day) than red deer when expressed in absolute terms, but not on a metabolic liveweight basis ($P > 0.05$). Liveweight gain during winter did not differ significantly between genotypes regardless of whether it was expressed in absolute or relative terms. Although not significant, relative liveweight gain (g/kg $^{0.75}$/day) was 14% greater for red than for hybrid deer.

During spring, hybrids consumed 260 g DM/head/day more on average than their red deer counterparts, but on a metabolic liveweight basis intake was similar. However, during spring hybrid liveweight gain was 1.63 g/kg $^{0.75}$ /day (approximately 60 g/day or 15%) greater than red deer ($P < 0.05$).

Table 4.2 *Mean intake and liveweight gain (standard error of mean in parenthesis) of housed red deer and hybrid weaner stags during winter and spring.*

			Winter	Genotype	Spring	Genotype	Season
Intake	g DM/h/day	Red	1627 (24)	*	2430 (55)	**	**
		Hybrid	1742 (28)		2690 (51)		
	g DM/kg $^{0.75}$ /day	Red	0.95 (0.01)	NS	1.09 (0.20)	NS	**
		Hybrid	0.92 (0.01)		1.11 (0.20)		
LWG	g/day	Red	168 (13.4)	NS	285 (16.4)	**	**
		Hybrid	162 (14.8)		345 (19.1)		
	g/kg $^{0.75}$ /day	Red	7.99 (0.51)	NS	10.70 (0.59)	*	**
		Hybrid	7.02 (0.57)		12.33 (0.56)		

Where; NS, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$;

There was a significant ($P < 0.05$) increase between winter and spring in both feed intake and liveweight gain for both genotypes. In absolute terms, red deer increased their intake 49% from winter to spring while hybrid intake increased 54%. The corresponding increases on a metabolic liveweight basis were 15 and 21%. This resulted in a seasonal increase in liveweight gain. Between winter and spring, red deer increased liveweight gain by 34% and hybrids by 76% on a metabolic liveweight basis.

4.4 Discussion

This study extends the findings of the previous experiment (Chapter 3) by examining intake and liveweight gain in two deer genotypes at *ad lib.* intake.

Intake and liveweight gain data from this and previously published studies are presented in Table 4.3. Generally, *ad lib.* intake and liveweight gain in winter and spring of red deer weaner stags were similar to those reported previously and contained similar between-season variation.

Table 4.3. *Previously published values for ad lib. intake and liveweight gain of housed weaner red deer stags during winter and spring.*

Author	Intake (MJ ME/kg $^{0.75}$/day)	Liveweight gain (g/day)
	Winter	
This study	**0.95**	**168**
Suttie *et al.* (1987)	0.70	80
Milne *et al.* (1987)	0.80	82
Suttie and Hamilton (1983)	0.90	141
Webster *et al.* (1997)	0.90	174
Brelurut *et al.* (1995)	0.81	241
	Spring	
This study	**1.09**	**285**
Suttie *et al.* (1983)	0.70	220
Milne *et al.* (1987)	1.18	198

Elk and hybrids

There are no equivalent liveweight gain data for housed, *ad lib.* fed hybrid deer. However, similar deer outdoors achieved a liveweight gain of 170 g/day on winter pasture and 310 g/day in spring on generous allowances of chicory (Kusmartono, *et al.*, 1995). Penned 6 month old wapiti grew at a rate of about 150 g/day in winter (Jiang and Hudson, 1994), which is similar to the penned red deer of Suttie and Hamilton, (1983). Spring liveweight gain for Canadian elk was 400-500 g/day (Jiang and Hudson, 1994). A comparison of wapiti x red F1 hybrids with red deer calves showed the average growth rate from weaning to 14 months was 37% higher for the hybrid (273 g/day) than for red deer (171 g/day) (Pearse, 1988).

These data suggests that the liveweight gains of 162 g/day during winter and 345 g/day during spring for hybrid deer in this experiment are similar to those reported in previous studies even though such studies have involved wapiti or elk and were collected in a grazing environment.

Seasonal effect

This work confirms results on pasture (Chapter 3) that there may be little difference between genotypes in liveweight gain during the winter but hybrids have a higher liveweight gain during spring compared with red deer. Essentially, hybrids appear to have a greater amplitude in the seasonal cycle of liveweight gain (Figure 4.1). The spring liveweight gain (400-500 g/day) of Canadian elk recorded by Jiang and Hudson (1994) suggests the seasonal amplitude in pure elk animals may be higher than hybrids.

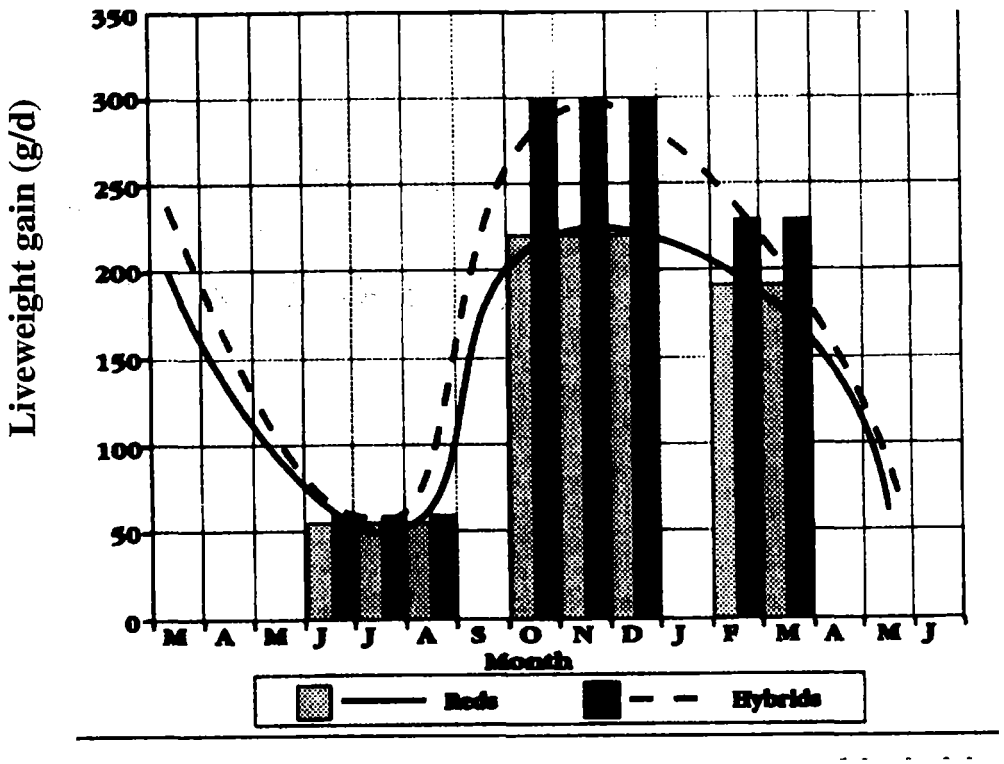


Figure 4.1 *The seasonal pattern liveweight gain of red deer and hybrids (data from experiment 1, Chapter 3)(lines fitted by hand).*

Liveweight gain prediction

To estimate the contribution of change in intake to change in liveweight gain between seasons, liveweight gain was predicted (Table 4.4) from the *ad lib.* intake recorded in this experiment (Table 4.2) assuming a common ME_m and cost of liveweight gain for genotypes and seasons. Using the average liveweight (kg) during the two experimental periods for each genotype and an estimate of the energy requirement for maintaining liveweight (ME_m) (0.57 MJ ME/$W^{0.75}$/day) (Fennessy *et al.*, 1981), the total energy requirement for maintenance of liveweight was calculated. The ME available for growth was obtained by subtracting ME_m from ME intake (where ME intake was the DM intake multiplied by the ME content of the feed, MJ ME/kg DM). An estimate of liveweight gain was

derived by dividing the energy available for growth (MJ) by an estimate of the costs of liveweight gain (37 MJ ME/kg gain) (Fennessy *et al.* 1981).

Table 4.4. *Predicted and observed liveweight gain (LWG) of red and hybrid deer in winter and spring based on average group liveweight and intake from individually penned animals and published values of ME_m and energy cost of gain (Fennessy et al., 1981).*

	Winter		Genotype Difference (%)	Spring		Genotype Difference (%)
	Red	Hybrid		Red	Hybrid	
Average liveweight (kg)	56.9	65.0		78.1	84.6	
Intake (MJ ME/W $^{0.75}$/day)	0.95	0.92		1.10	1.11	
Maintenance (MJ ME/W $^{0.75}$/day)	0.57	0.57		0.57	0.57	
Cost of gain (MJ ME/kg)	37	37		37	37	
Predicted LWG (g/W $^{0.75}$/day)	10.3	9.5	+8	14.3	14.6	-2
Predicted LWG (g/day)	213	217	+2	376	407	+8
Observed LWG (g/W $^{0.75}$/day)	7.99	7.02	+14	10.7	12.3	-13
Observed LWG (g/day)	168	162	-3	285	351	+23
Observed – Predicted difference (%)	29	35		34	19	
Difference (%) (predicted LWG - observed LWG)	32			27		

Where;
genotype difference is the difference between red and hybrid deer expressed as a percentage of the hybrid value with positive values representing higher red liveweight gain and negative values representing higher hybrid liveweight gain and
predicted LWG - observed LWG differences was the difference between predicted LWG (g/W $^{0.75}$/day) and observed LWG (g/W $^{0.75}$/day) expressed as a percentage of observed LWG (g/W $^{0.75}$/day).

Seasonal effects

Observed liveweight gain in both winter and spring was greater than was predicted using a common ME_m and energy cost of liveweight gain for both genotypes. Predicted liveweight gain from this model was 32% higher in winter and 27% higher in spring than the observed liveweight gains. Therefore, there is some basis for rejecting common ME_m and/or cost of liveweight gain values for both winter and spring.

Higher predicted liveweight gain values relative to observed values could have been a result of;

1) underestimation of ME intake
2) underestimation of ME_m
3) underestimation of the energy costs of gain

Estimates of ME intake are based on ME/DE value estimated from proximal analysis of feed which do not always provide reliable estimates for compound feeds (Isherwood *pers. com.*). However, the ME/DE values used for calculating ME intake are what would be expected based on the feed table values of the diet constituents and their relative proportions (see Chapter 5 for a full discussion on estimating ME intake). Therefore, there is little evidence that ME intake was overestimated.

The maintenance requirement and energy cost of gain figures reported by Fennessy *et al.* (1981) were derived from similar animals, housed indoors on a similar feed source. The values used were similar to other studies (Brockway and Maloiy, 1968; Suttie *et al.*, 1987; Semiadi *et al.*, 1994) and there is no good evidence to suggest they were overestimated.

Genotype effects

Observed differences between genotypes in liveweight gain were greater (13 - 14%) than was predicted using different liveweights but common ME_m and energy cost of liveweight gain values for both genotypes (2 - 7%).

In this model, predicted winter liveweight gain was 7% higher for red deer compared with hybrids however, they actually gained liveweight 14% faster than hybrids. In spring, the opposite occurred where predicted liveweight gain was similar between genotypes but hybrids actually gained liveweight 13% faster than red deer. This mismatch between predicted and observed values suggests that red and hybrid deer do not share a common ME_m and/or liveweight gain cost.

Further, the discrepancy between calculated and observed spring liveweight gain was greater for red deer (106 g/day) than hybrids (56 g/day) suggesting that the estimates of ME_m and/or costs of liveweight gain were too low, and that red deer appear to grow more slowly during spring than would be predicted.

Of the 66 g/day difference between genotypes in spring liveweight gain observed in this study, 27 g/day (40%) can be explained by the difference in average liveweight between genotypes over the experimental period. The remainder is possibly a result of a genotype difference in the energy required for maintenance and/or the energy cost of liveweight gain

Conclusions

During winter, both red deer and hybrids had similar DMI intake when expressed on a metabolic body weight basis but liveweight gain tended to be higher for red than for hybrid deer but lower than was predicted using previously published values of ME_m and cost of liveweight gain. Although differences were non-significant, there was some suggestion that red and hybrid deer differ in either their energy requirements for zero liveweight gain or the energy costs of liveweight gain in winter.

During spring, while *ad lib.* intake expressed on a metabolic body weight basis was not different between genotypes, red deer grew more slowly than hybrids. The difference in liveweight between genotypes was able to explain about 40% of the difference in absolute liveweight gain but the remainder must be accounted for by differences in maintenance requirement and/or the energy cost of gain.

Chapter 4b

Effect of season on feed intake and liveweight gain of individually penned young red deer (*Cervus elaphus)* and red x elk hybrid stags

4.6 Introduction

When offered *ad. lib.* feed during spring hybrids exhibit a greater liveweight gain on an absolute basis compared with red deer. While 40% of the advantage could be explained by genotype differences in liveweight (Chapter 4a), the remaining variation in liveweight gain appears not to be attributable to differences in intake since in this study relative intake was similar for both genotypes.

An increased maintenance requirement of animals affects liveweight gain by reducing the proportion of total metabolisable energy intake (MEI) available for growth, assuming it is not accompanied by a increase in feed intake. A lower mean ME_m over a 12 month period have been reported for the tropical sambar compared with red deer in New Zealand (Semiadi *et. al.*, 1994). However in this study, average liveweight gain for the whole year did not differ between genotypes which is probably reflects the lower feed intake of sambar deer. A similar study with bovine animals also showed a lower maintenance heat production in tropical bovine *(Bos indicus)* compared to temperate bovine *(Bos taurus)* (Vercoe 1970). The lower maintenance requirement may be an adaptive strategy to reduced heat production to counter high environmental temperatures in a tropical climate (Semiadi *et. al.*, 1994). Currently it is unclear whether maintenance requirements differ between two temperate deer genotypes.

There is a considerable amount of literature which shows the requirement for maintenance increases from winter to spring/summer for red deer (Simpson *et. al.*, 1978b), wapiti (Jiang and Hudson, 1994) and white tailed deer (Thompson *et al.*, 1973). Whether this reflects an intrinsic seasonal cycle of fasting heat production or an increase in metabolic rate associated with an seasonal increase in feed intake, or activity is less well established.

For adult white tailed deer, fasting metabolic rate increased from winter (406 $kJ/kg^{0.75}$/day) to summer (600 $kJ/kg^{0.75}$/day) (Silver *et. al.*, 1969). However, more recent investigation with white tailed deer (Pekins and Kanter, 1992) and wapiti (Jiang and Hudson, 1993) suggests fasting heat production does not change with season.

The aim of this experiment was to identify if red and red/elk genotypes differed in maintenance requirement and therefore was a cause of differences in liveweight gain performance of young red deer and hybrids in spring.

4.7 Material and Methods

Experimental design

Red and hybrid weaners stags (n=10) were housed during winter (3 June - 27 August) and spring (16 October - 16 December). Deer were randomly assigned to one of five feeding treatments which ranged from approximately maintenance to near *ad lib.* intake. Daily DM intake and weekly liveweight gain was recorded for each deer.

Animals

Five red and five hybrid weaner stags were housed in separate pens (3.5 m^2) during 85 days in winter and 61 days in spring. The animals used in this experiment were cohorts of those used in the experiment described in Chapter 4a and received similar copper and anthelmintic treatment. At the beginning of the winter experiment deer weighed 50.6 ± 1.1 kg and 58.1 ± 0.4 kg (mean ± SD) for red deer and hybrids, respectively. Deer were housed for 10 days prior to start of data collection in each season. Deer were fed daily at 0900 h and were weighed (to the nearest 0.1 kg) weekly prior to feeding using the equipment described in Chapter 4a.

Feeding

One individual from each genotype was randomly assigned to one of 5 feeding treatment (Table 4.5). The feeding treatments were 0.5, 0.6, 0.7, 0.8, or 0.9 times estimated *ad. lib.* intake where *ad. lib.* intake was estimated as 1.5 and 1.7 kg DM/head/day during winter and 3.0 and 3.3 kg DM/head/day during spring for red deer and hybrids, respectively. This estimate was based on data collected in the pre-experimental period. Daily feed allowance was adjusted for changes in liveweight on a weekly basis. Deer had access to water at all times through drinking nozzles and were fed the same diet to those deer in Chapter 4a (Table 4.1).

Actual DM intake was defined as the difference between feed offered (kg DM) and feed refused (kg DM). Dry matter content of feed and feed refusals were as described in Chapter 4a.
Energy intake was estimated by multiplying DM intake by the ME concentration (12.0 MJ ME/kg DM) of the feed. ME values of the feed were estimated using the equation for compound feed stuffs (AACR, 1990) as in Chapter 4a.

Table 4.5 *Feeding treatments (g DM/$W^{0.75}$/day) for deer in winter and spring.*

	Winter		Spring	
Treatment (x *ad lib.* intake)	**Red**	**Hybrid**	**Red**	**Hybrid**
0.5	37	41	41	42
0.6	45	49	54	55
0.7	53	58	68	69
0.8	60	66	81	83
0.9	68	74	94	96

Statistical Analysis

Mean daily liveweight gain was defined as the regression coefficient of the linear relationship between liveweight (kg) measured weekly and time (days) and expressed as grams/day. Relationships between intake and liveweight gain were fitted using linear regression. Regression coefficients and intercept values were tested for differences between relationships for each genotypes using the method of Snedecor and Cochran (1999).

4.8 Results

Intake and liveweight gain

The mean daily ME intake (calculated from DM intake) and corresponding liveweight gain of individually penned deer for winter and spring is given in Figure 4.2 Within each genotype, linear relationships between liveweight gain (g/$W^{0.75}$/day) and intake (MJ ME/$W^{0.75}$/day) were fitted to winter and spring data. These relationships were not significantly different in either regression coefficient or intercept value ($P > 0.05$) indicating the response of liveweight gain to intake was independent of season. However, when data from both seasons were combined there was a significant difference ($P < 0.05$) between genotypes in intake when liveweight gain was zero indicating ME_m was greater for hybrids than red deer. The relationships were;

Red deer	LWG (g/$W^{0.75}$/day) = 14.9 (1.8) ME Intake – 5.8 (1.5)	R^2 = 89%
Hybrid deer	LWG (g/$W^{0.75}$/day) = 19.3 (1.5) ME Intake – 11.2 (1.8)	R^2 = 94%

To maintain liveweight during either season, hybrids required a higher intake (0.59 MJ ME/W $^{0.75}$ /day) compared with red deer (0.39 MJ ME/W $^{0.75}$/day). Consequently, when intake of both genotypes was restricted to a similar relative level (less than 1.0 MJ ME/W $^{0.75}$/day) red deer grew faster than hybrids. The cost of liveweight gain (mean of both seasons) was 67.5 and 52.4 MJ ME/kg for red deer and hybrids respectively but was not significantly different.

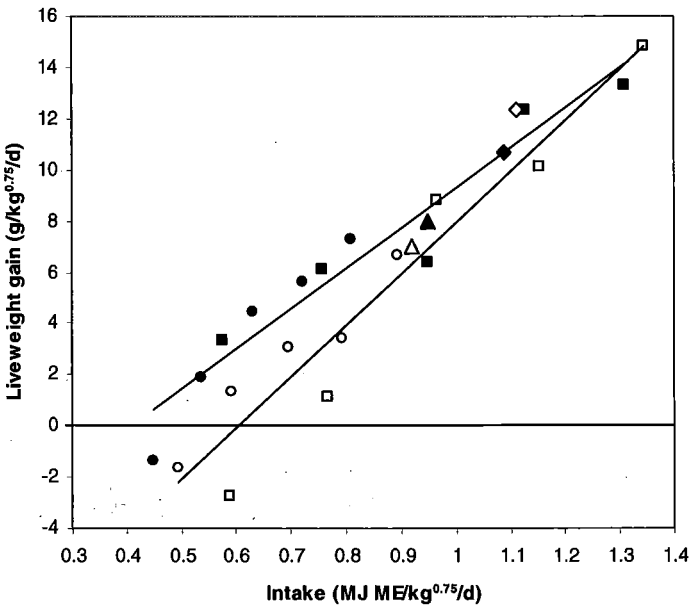


Figure 4.2 *The intake and liveweight gain of individually penned red (solid symbols) and hybrid (open symbols) deer during winter (●) and spring (■). Values from ad lib. group fed deer for winter(▲) and spring (◆)(Chapter 4a) are also shown but not included in the regression Fitted lines are for genotype.*

For both genotypes a quadratic polynomial function was also fitted since red deer appeared to reduce their liveweight gain response to increasing intake to a greater extent than hybrids at intake greater than approximately 0.6 MJ ME/W $^{0.75}$/day. The equations were;

Red Deer LWG (g/W$^{0.75}$/day) = -13.3 (4.7) +33.4 (11.4) x – 10.4(6.3) x^2 R^2 = 94%

Hybrid Deer LWG (g/W$^{0.75}$/day) = -13.9 (5.8) +25.3 (13.5) x –3.3 (7.2) x^2 R^2 = 93%

where x = MJ ME/W $^{0.75}$/day

and figures in parenthesis are standard errors

Based on these relationships, maintenance requirement was 0.47 MJ ME/W $^{0.75}$/day and 0.60 MJ ME/W $^{0.75}$/day for red and hybrid deer, respectively. The liveweight gain of group fed deer in the previous experiment was generally similar to that of individually penned deer offered the same intake.

4.9 Discussion

Maintenance Requirement

The ME requirement for maintenance estimated from previous studies are presented in Table 4.6.

Table 4.6. *Previously reported values of energy requirement for maintenance (kJ ME/W$^{0.75}$/day) for penned red deer and wapiti during winter and spring.*

Author	season	ME_m	genotype
This study	winter/spring	470	red deer
Simpson *et al.* (1978b)	winter	450	red deer
	summer	500	red deer
Fennessy *et al.* (1981)	winter	570	red deer
Suttie *et al.* (1987)	winter/spring	520	red deer
Semiadi *et al.* (1994)	12 months	630	red deer
This study	winter/spring	600	hybrids
Jiang and Hudson, (1992)	winter	572	wapiti
Jiang and Hudson, (1994)	winter	473	wapiti
	summer	728	wapiti
Cool and Hudson, (1996)	winter	560	wapiti

Maintenance requirements for hybrid deer are similar to those reported for wapiti in winter. The estimate of maintenance for red deer derived in this study is low however, compared with some previous estimates.

The magnitude of the difference (0.13 MJ ME/W $^{0.75}$/day) is similar to that reported between young sambar (*Cervus unicolor*) and red deer (0.10 MJ ME/W $^{0.75}$/day) with sambar having the lower maintenance requirement (Semiadi *et al.*, 1994, 1998). If these differences in ME_m are incorporated into the liveweight gain calculation used in Chapter 4a, it would predict a 2.8 g/W $^{0.75}$/day or 65 g/day difference (based on the mean liveweight of each genotype) in liveweight gain in favour of red deer during spring at *ad lib.* intake. This calculation suggests that at *ad lib.* intake, provided the composition and efficiency of liveweight gain are the same for each genotype, red deer should gain liveweight at a faster rate than hybrids, which is contrary to what was recorded in this experiment and Chapter 4a. Although Semiadi *et al.*, (1994) reported ME_m differed between red and sambar deer, liveweight gain was not significantly different due to sambar having a lower voluntary feed intake compared with red deer. Although intake was similar between genotypes in Chapter 4a it is possible that hybrids were able to gain liveweight faster than red deer at a similar intake despite a greater ME_m due to other effects. These include (1) greater ME intake through higher digestibility, (2) differences in the partial efficiency for fat (k_f) and protein (k_p) deposition, or (3) differences in the composition of gain and therefore a difference in the energy value of gain. These factors have been investigated in Chapter 5. Based on this data there was no seasonal difference in the intake-liveweight gain relationship for each genotype. This is in contrast to many studies which

have reported a seasonal increase in ME_m from winter to spring. There is some evidence in Figure 4.2 that if more data were available for hybrids especially, liveweight gain in spring may have been significantly lower than in winter at the same intake.

The major component of maintenance requirement is fasting heat production (FHP). There is some evidence for a seasonal cycle in FHP (Silver *et al.*, 1969; Thompson *et. al.*, 1973) although others have found no difference between winter and summer FHP (Pekins and Kanter, 1992). Differences in ME_m between genotypes could result from either (1) a different amplitude in the seasonal cycle of FHP between red deer and hybrids or (2) a different FHP *per se* or (3) the same FHP but a different composition of body weight change.

Seasonal cycles in FHP

Seasonal metabolic rate cycles have been reported for moose, elk, roe deer, white tailed deer and red deer although the amplitude of seasonal change reports is variable (10-50%). However it is unclear from these reports whether this seasonal cycle results entirely from an intrinsic cycle in FHP or seasonal cycles in intake and liveweight gain which both affect metabolic rate. While there is some evidence that FHP is lower in winter than summer (Silver *et al.*, 1969), the more recently published literature discredits these earlier findings, citing non-thermoneutral environments and activity within the calometric chamber (Pekins and Kanter, 1992) and feed intake (Nilssen *et al.*, 1984) as likely causes of the increased metabolic rate during spring. Although FHP should be measured when there is little or no digestive processes occurring, high previous levels of nutrition have a positive effect on FHP. Therefore, it is likely seasonal variation in intake confounds seasonal variation in FHP. Where intake increased from winter to summer for wapiti (Jiang and Hudson, 1993), summer FHP tended to be higher in spring compared with winter, although the differences were not significant. However, in the current experiment feeding treatments were a constant proportion of *ad lib.* and therefore might have been expected to minimise any confounding effects of seasonal variation in intake on FHP. In this situation any seasonal effect on FHP *per se* should have resulted in a different seasonal ME_m on the same intake. However, there was no difference in ME_m between seasons (Figure 4.2) and therefore this observation would agree with those of Pekins and Kanter (1992) and Nilssen *et al.* (1984) that there is no important intrinsic seasonal cycle in FHP other than that caused by intake. Although the results from this study are consistent with there being no seasonal cycle in FHP, ME_m could still be lower for red deer compared to hybrids as a result of a difference in FHP between genotypes independent of both season and intake. A previous author has shown different species (sheep vs cattle) and different genotypes (Ayrshire vs Aberdeen Angus) (Blaxter, 1989) have different levels of fasting heat production. Although FHP was not measured in the current experiment, it is likely, since the majority of ME_m is FHP (Blaxter, 1989), that at least some of the genotype difference in ME_m is likely to be attributed to differences in FHP.

It is possible that genotypes with a similar FHP could still have a different ME_m depending on the composition of negative gain to supply energy for FHP. For example, to supply FHP of 270 $kJ/W^{0.75}$ /day would require less liveweight loss if the loss was all fat (10 g) compared to a solely lean loss (64 g) assuming k_m to be 0.7 and the energy value of adipose and lean as 39.5 and 6 MJ/kg DM, respectively. There is little difference in k_m irrespective of whether catabolism is predominantly fat or protein. Different genotypes could potentially have a different ME_m for liveweight maintenance but because they lose one tissue and gain another at different rates may have a similar ME_m for energy balance. Although results from this study indicate genotypes differ in ME_m for liveweight maintenance it is unclear whether they differ in ME_m for zero energy balance.

Activity

Seasonal increases in maintenance requirement in free ranging deer have been linked to increases in activity associated with walking and foraging for food (Pauls *et al.*, 1981). In previous studies (Jiang and Hudson, 1992) where seasonal variation in maintenance requirements has been recorded, deer have not been housed and it is possible these deer were more activity during spring compared with individually penned deer which had limited opportunity for activity. Penned deer in this experiment each had an equal opportunity to move as pens sizes were the same and therefore energy requirement for activity are likely to have been similar between genotypes. Although there was no formal record of deer activity while individually penned, routine observations and unpublished resting heart rate data suggest there was no obvious seasonal difference in activity and no difference between genotypes The greater liveweight gain of individually housed deer (Chapter 4b) compare with group fed animals (Chapter 4a) at the same DM intake is an observation consistent with a negative effect on liveweight gain of increased movement through increasing pen size. At a similar intake deer housed in individual pens accumulated liveweight at a faster rate than those in Chapter 4a which were housed in groups. A possible explanation for this is that deer housed in groups had greater areas in which to move (3.5 v 58.5 m^2) and were allocated a greater area per head than those individually penned (3.5 vs 3.9 m^2) and therefore had a greater opportunity for movement and interaction with other deer which routine observations suggest they took advantage of. Since increases in movement have been shown to increase energy expenditure (Pauls *et al.*, 1981) it is possible this was responsible for a lower rate of liveweight gain in deer housed in groups.(Blaxter, 1989) calculated that sheep expend about 3 J for every kg of body weight moved 1m. On this basis a 100 kJ difference (about the difference in ME_m required for the difference in liveweight observed) would result from deer in large pens walking 120 m more than those in individual pens

In contrast, recent research (Hanlon *et. al.*, 1997) reported deer housed in individual pens which gave restricted visual and tactile contact with other deer had a lower mean liveweight gain (138 g/day)

than deer housed in groups (202 g/day) despite little difference in feed intake between treatments. Although deprivation of social contact changed behaviour (more time lying and less time eating and grooming) there appeared to be no difference in stress levels as indicated by cortisol levels. For our individually penned deer, intake depression did not seem to occur since deer offered feed *ad lib.* had higher liveweight gain than those group fed *ad lib.* The design of the individual pens used in this experiment allowed for both visual and tactile contact between animals in adjacent pens may have reduced the effect of individually penning animals seen by Hanlon *et al.* (1997).

4.10 Conclusion

Although there appeared to be a difference between genotypes in the energy required to maintain liveweight, some estimates of ME_m were low (especially for red deer) and based on a limited sample size which make any conclusions tentative. Further, it is unclear whether ME_m for energy balance differs between genotypes and therefore ME_m for liveweight maintenance differences could be explained by a different composition of body weight change.

Hybrids appear to have higher maintenance requirements than red deer but this was unable to explain any of the differences in *ad lib.* liveweight gain since, all else being equal, red deer should have accumulated liveweight gain at a faster rate compared with hybrids.

There is some evidence that genotypes differ in their composition of gain with the liveweight gain response to increasing intake differing for red deer and hybrids. As ME intake increased the marginal rate of liveweight gain decreased for both species but more so for red deer than hybrids. This suggests that a least some of the difference in liveweight gain between genotypes may have been a result of a rate of gain effect between genotypes on the composition of gain.

Chapter 5a

Comparative body composition of red deer *(Cervus elaphus)* and red x elk hybrids *(Cervus elaphus spp).*

5.0 Introduction

The experiment reported in Chapter 4a showed that red and hybrid deer offered feed *ad lib.* during winter had similar liveweight gain and intake when expressed on a $W^{0.75}$ basis. During spring however, hybrids gained liveweight faster compared to red deer but maintained a similar relative intake. Although red deer appeared to have a lower ME requirement for liveweight maintenance (Chapter 4b) it was low compared to other estimates (Fennessy, 1981; Suttie *et al.*, 1987) and therefore required validation. It was also unclear whether the lower ME requirement for liveweight maintenance in red deer translated into a lower ME requirement at zero energy balance or alternatively that the composition and therefore the energy value of liveweight change was different between genotypes.

The experimental approach was to use CT imaging to determine the change in fat, protein and therefore energy content of individual deer as liveweight changed over a range of energy intakes. This chapter (Chapter 5a) presents the body composition data and Chapter 5b presents the implication of changes in body composition on the energy metabolism of both genotypes.

5.1 Materials and methods

Experimental design

Red deer and hybrid weaner stags were housed in individual pens for a period of 7 weeks in both winter (July - August) and spring (October - December). Within genotype, deer were stratified according to liveweight and paired so that, within each pair, deer were of a similar pre-experimental liveweight. Pairs within each genotype were then randomly allocated to one of 7 feeding levels which ranged from approximately maintenance to *ad lib.* Maintenance was assumed to be 0.52 MJ ME/W $^{0.75}$/day as reported for hybrid deer in Chapter 4b. During each 7 week experimental period liveweight gain and DM intake were measured. Immediately prior to, and at the conclusion of each 7 week period, body composition was estimated using a computer-assisted topography scan (CT scan).

Animals

Fourteen red deer weaner stags of mean liveweight 59.0 ± 1.0 kg (± SEM) and 14 hybrid weaner stags of mean liveweight 69.0 ± 1.3 kg (± SEM) and approximately 8 months old were used in the experiment. Deer were obtained from two commercial farms and brought to the Lincoln University Deer Research Unit in late June. Deer were set - stocked on short pasture for a period of two weeks prior to the start of the winter experiment and fed increasing amounts of concentrate feed (APR Plus, Target Stock Feed, Archers Milling Company, Rangiora, NZ.). At the start of the winter experiment deer were weighed, drenched with Vetdectin pour-on (Cydectin New Zealand Ltd) at a rate of 1 ml/10 kg and given a 5 g copper oxide bolus (Copacaps, Rhone Merieux). Animals were housed in randomly allocated individual pens (3.5 m^2) with unlimited access to water. Liveweight, to the nearest 0.5 kg, was recorded on a weekly basis.

Feeding

Deer consumed either 35, 40, 45, 50, 55, 65 g DM/kg LW $^{0.75}$/day or *ad lib.* feed of a grain based concentrate ration. The raw ingredients and proximal analysis of feed are given in Table 5.1. A ration based on individual liveweight and feeding level was offered daily to each animal between 0900 h and 1000 h. Daily rations were altered weekly to account for any increase in individual liveweight during the experiment. The previous days refusals were collected, weighed and discarded prior to feeding.

Animals assigned to the *ad lib.* feeding treatment were fed such that refusals were no less than 20% of the total offered. Increases in feed offered to *ad lib.* fed deer occurred when refusals for the preceding two days were less than 20% of that offered.

Table 5.1. *Raw ingredients and proximate analysis (DM basis) of the grain-based pelleted diet*[1] *offered to red and hybrid deer during winter and spring.*

Ingredients	**g/kg DM**
barley grain	468
bran/pollard	460
molasses	8
$CaCO_3$	30
NaCl/selenium premix	34
Analysis	**g/kg**
dry matter	872
organic matter	923
crude protein	142
fat	36
acid digestible fibre	111
dry matter digestibility	831
organic matter digestibility	895
M/D (MJ ME/kg DM)[2]	11.7

1. All-purpose ration (APR plus) Target Stock Feed, Archers Milling Company, Rangiora, NZ.
2. Calculated from the equation for compound feed stuffs (AACR, 1990).

MEI estimation

Daily ME intake was calculated by multiplying DMI/day (kg) by ME/DE (MJME/kg DM). ME/DE was estimated from proximal analysis of feed using the relationship for compound feed stuffs (AACR, 1990) and was 11.7. MJME/kg DM

Computer tomography

Computer-assisted tomography (CT) and the Cavalieri principle (Gundersen *et al.*, 1988) were used to estimate the volume of adipose, lean and bone tissue in the live animal. Tissue volumes were subsequently converted to individual tissue mass. The Cavalieri principle states that an unbiased estimate of volume of a 3 dimensional, irregularly shaped object can be achieved by measuring the cross-sectional area of the object at equal spacing along the length of the object assuming the position of first slice is chosen at random. Shape and orientation of the object have no effect on the accuracy of volume estimation but errors in the estimation of volume decrease as the number of cross sections increases. Previous authors (Roberts *et al.*, 1993) have reported coefficients of variation of less than 5% for estimates of individual muscle volume based on 10 -15 cross sections.

Animal handling

Feed was withheld from deer for 12 h prior to scanning. Deer were sedated with 1.0 mg/kg liveweight of xylazine hydrochloride 5% i.m. (Thiazine 50, Virbac Laboratories Ltd) and 4 ml pentothal (Virbac Laboratories Ltd) i.v. and were placed in ventral recumbency in a wooden scanning box (Plate 5.1). They were secured into the box with straps and were fitted with a hood over the head. On the completion of scanning each animal received yohimbine (1 ml/head) (Reversal, Virbac Laboratories

Ltd) and were allowed to recover for 2 - 3 h in a small holding pen before being returned to individual pens. The procedure from sedation to release lasted approximately 50 minutes per animal and for each scanning period all deer (n = 28) were scanned in random order over 4 days. All procedures met Lincoln University Animal Ethics Committee requirements.

Image capture

A Technicare Deltascan 2020 - G CT scanner (Technicare Corporation) was used. Images were captured using scanning voltage settings of 120 kV, 100 mA current, 5 mm slice thickness, 4 second scan time, 512 x 512 image matrix, a scanning circle of 50 cm and a normal filter for image reconstruction. Images were archived to 1/2 inch, 1600 bpi, 2400 inch tapes and subsequently transferred to a PC system.

The first cross sectional image on each deer was taken from a random site in the upper neck region (2^{nd} or 3^{rd} cervical vertebrae). Subsequent images (approximately 18) were taken at 54 mm (winter measurements) or 60 mm (spring measurements) intervals along each animal to form a scan sequence (Plate 5.2).

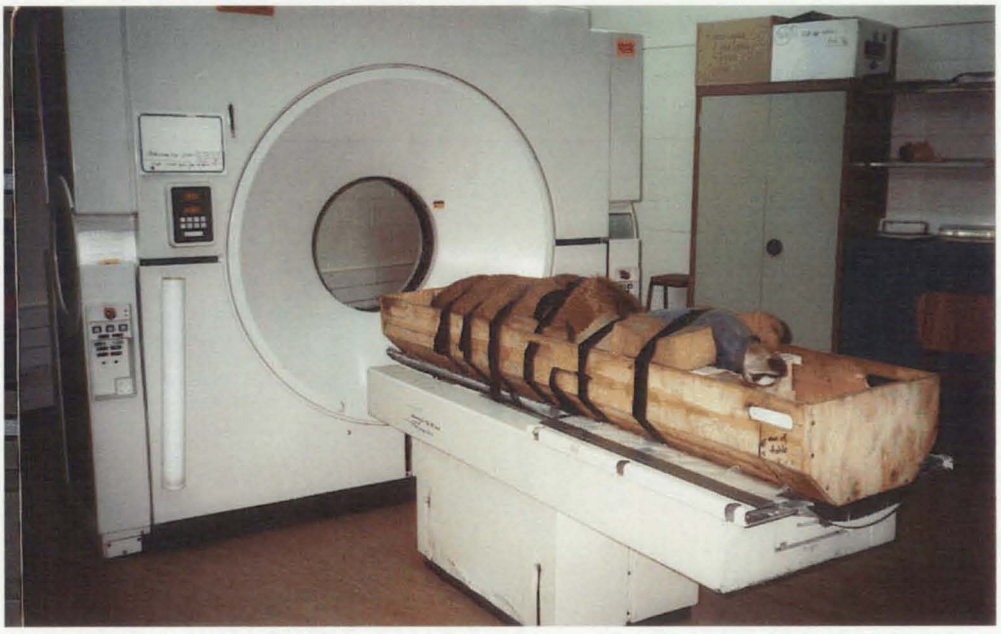


Plate 5.1. *Deer, laterally recumbent, secured by straps and supported by foam rubber in the wooden box prior to scanning.*

Image preparation

CT images were converted from their native format to a standard PC bitmap format using *Bitman* software (N.P Jopson *pers comm.)* which collapsed 512 Houndsfield units into a 256 grey scale. The resulting bitmaps, referred to here as "raw" CT images, were imported into imaging software (*Photomagic*, Micrografx Inc) and non - animal material such as the scanning box and straps and muddied pelage were electronically removed by making the associated pixels 100% black (0 grey scale). These images were termed "refined" images (Figure 5.1) Areas within the "refined" images corresponding to specific organs were subsequently removed to achieve empty body and carcass images (see Figure 5.1 and Plate 5.3).

The repeatability of operator removal of non - animal and non - carcass material for both carcass and whole body analysis was determined on 3 separate occasions during image analysis and was never less 0.99.

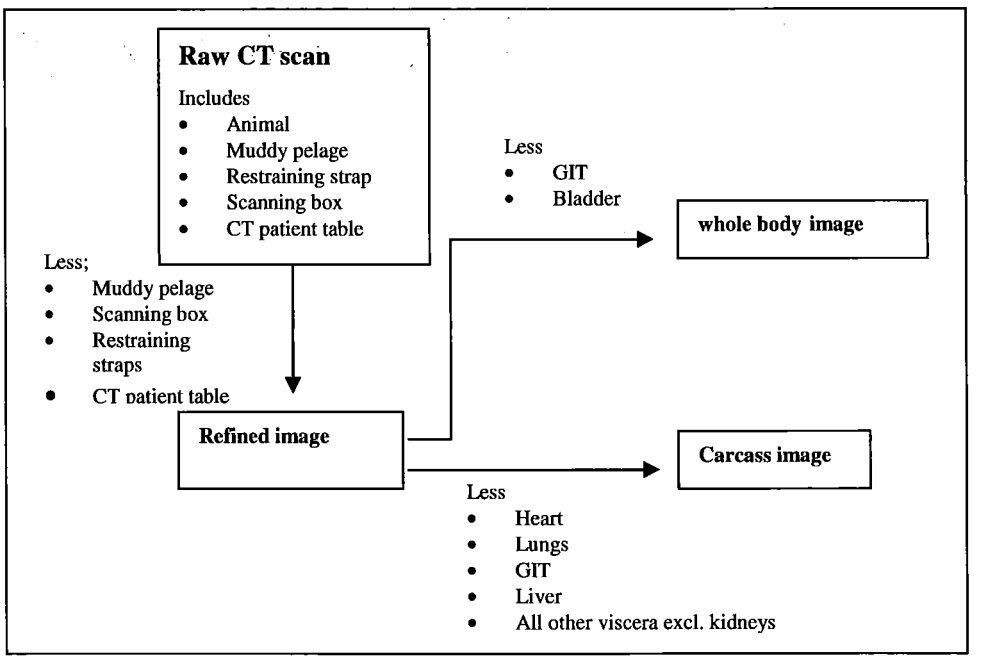


Figure 5.1 *A diagram illustrating the non - animal material removed to create refined images and the internal organs removed from refined images to create whole body and carcass images.*

Selection of images for analysis

Not all images captured in the scan sequence were used for analysis. On each deer the first image from the scan sequence to be included was that immediately anterior of the one which first showed thickening of the neck into the shoulder muscles (see Plate 5.2). Subsequent images 54 mm (winter) or 60 mm (spring) apart were included from this point until the final image. The final image included was that image in the scan sequence immediately anterior to the tail image. The tail image was defined as the image which contains only the tail and probably hind hocks. If any rump occurred with the tail in an image then the image immediately posterior to this was considered the tail image.

Dissection into individual tissues

Whole body and carcass images were "electronically dissected" into adipose, lean and bone area (*Autocat*, N.P Jopson *pers com*). The range of grey scales on which *Autocat* based its dissection were 35-120, 121-220 and 221-255 for adipose, lean and bone tissue, respectively. These ranges were established by creating a grey scale frequency distribution of all pixels in 3 images (shoulder, 12^{th} lumbar vertebra and rump) from 2 deer and identifying the grey scale value which most successfully separated the individual tissue distributions. Details on the validation of grey scale ranges are presented in Appendix III.

Conversions of tissue area to weight

Volume of adipose, lean and bone tissue in individual deer was calculated by multiplying the total area of each tissue (cm^2) from all images included in the analysis by the distance between images (cm). Tissue volume (cm^3)was converted to tissue mass using the standard densities for adipose, lean and bone tissue of 0.925, 1.031, and 1.549 kg/l respectively (Jopson, *pers. com*).

Plate 5.2. *A typical scan sequence of 'refined' images used in body composition analysis (**body sequence**).*

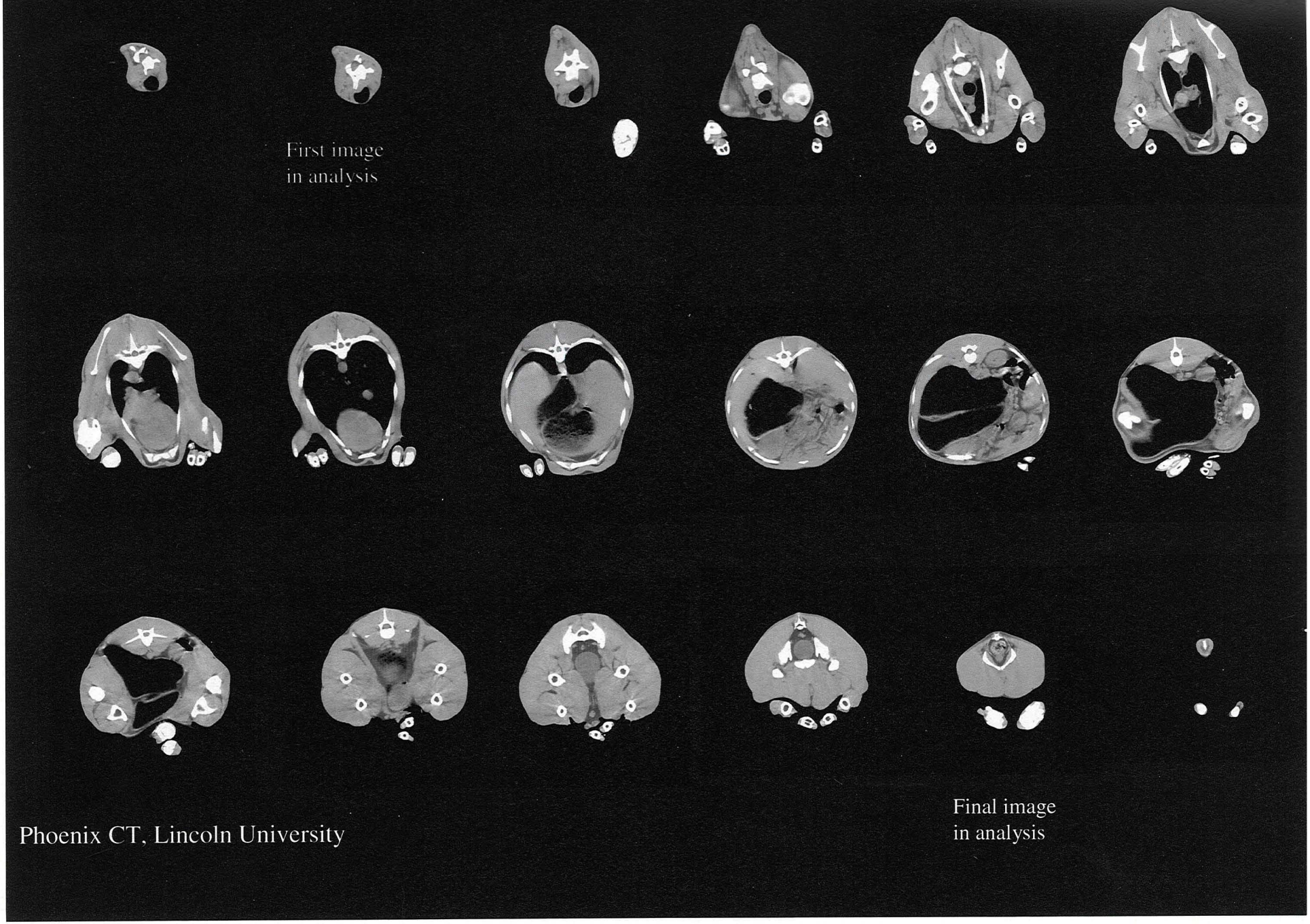
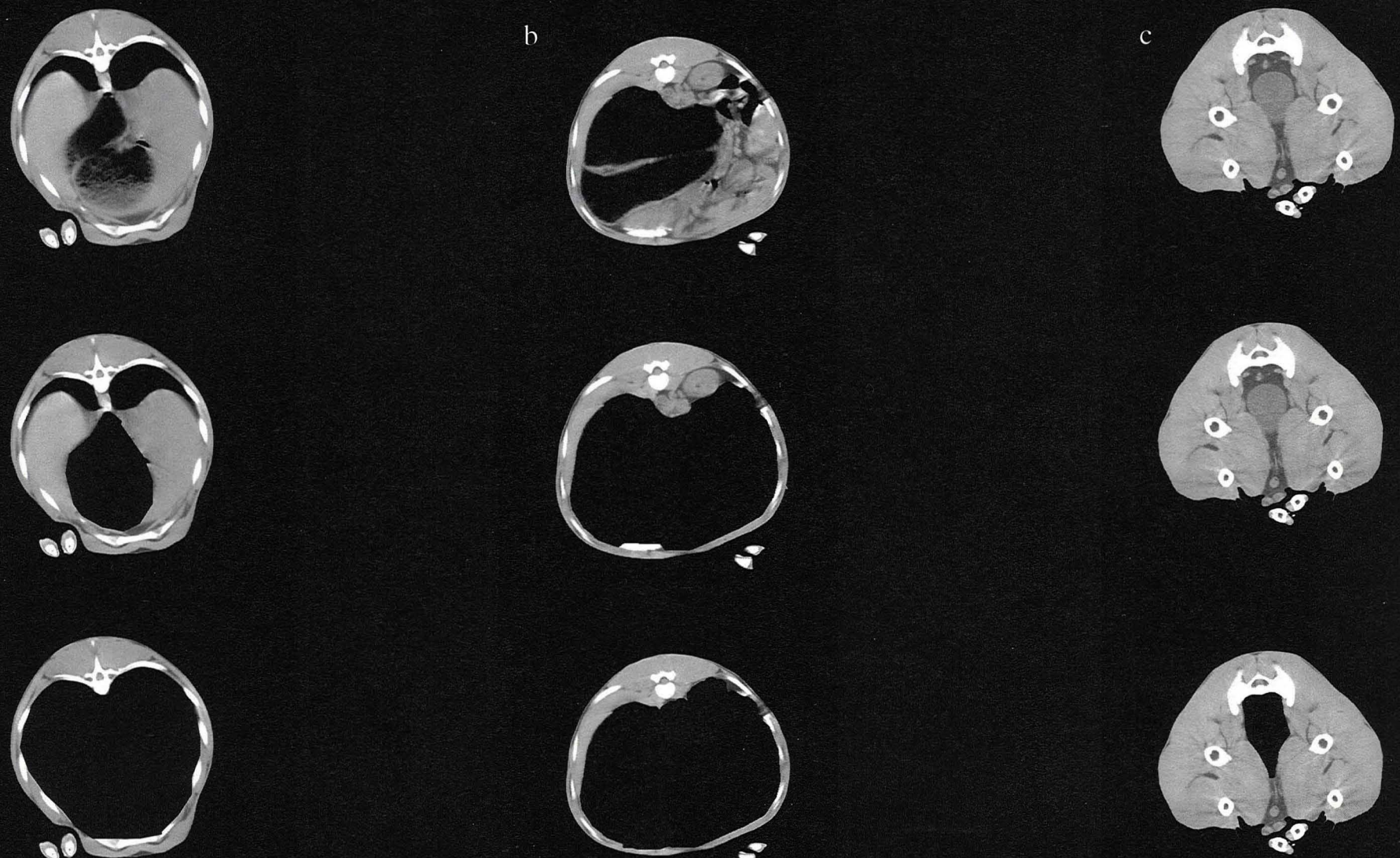


Plate 5.3 *Examples from the upper abdominal (a), lower abdominal (b) and pelvic (c) regions of refined (1), whole body (2) and carcass (3) images from which composition data was derived.*



Phoenix CT, Lincoln University

Whole body analysis

Whole body images were used to calculate the change in individual tissue weight over the experimental period. However, because it was necessary to remove GIT from whole body images during image processing, an estimate of fat and protein mass in empty GIT was added to whole body mass for this analysis. Estimation of fat and protein in empty gut was achieved in two stages. (1) the fresh mass of empty GIT (g) for all deer was estimated using GIT fresh mass recorded for 14 deer slaughtered at the conclusion of the trial and its relationship with whole body weight estimated from CT images (Figure 5.2). (2) estimates of GIT fresh mass were multiplied by an estimate of the proportion of fat and protein in empty GIT. Viscera, which included gastrointestinal tract, contained 5.4 g fat and 14.7g of protein per 100g of fresh weight in newly born lambs (Jagusch *et al.*, 1970) These data were assumed to approximate deer gastrointestinal tract composition.

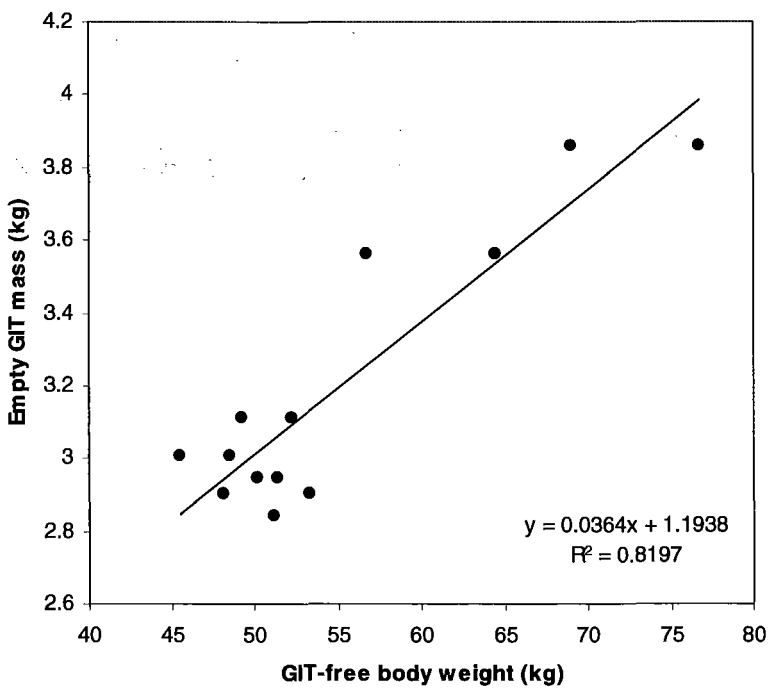


Figure 5.2 *The empirical relationship between empty fresh GIT mass (recorded at the conclusion of the spring experiment) and CT-estimated GIT free body weight for both red and hybrid deer (n = 14).*

CT estimated liveweight

Liveweight of deer was estimated using CT scans to provide a check on image capture and analysis. CT - estimated liveweight was calculated from a scan sequence in the same way whole body weight was derived except that "refined" images (see section image preparation section) were used instead of whole body images.

Statistical Analysis

The relationships between log whole body weight and log adipose, lean and bone tissue weight were fitted using linear regression. Differences in regression coefficients and intercept values between allometric growth equations for each genotype were tested using the method of Snedecor and Cochran (1980).

5.2 Results

Tissue weight change

Whole body images were used to calculate the change in individual tissue during winter and spring and are shown in Table 5.5 and 5.6, respectively.

At low levels of feeding (37.5 - 41.7 g DM/W $^{0.75}$ /day) deer lost adipose tissue in both winter and spring and lean in spring. As feeding level increased beyond 41.7 g DM/W $^{0.75}$ /day, generally there was a net gain of adipose and lean tissue gain increased.

During winter, total liveweight change ranged from -0.5 kg to +12.3 kg and the combined weight of total body tissues (estimated from CT images) from -0.16 to +8.6 kg. During spring, liveweight change ranged from -0.75 to 19.5 kg and combined tissues from -7.46 to 18.9 kg but changes in liveweight and whole body weight were not always well correlated. For example, red deer offered 41.7 g DM/kg LW $^{0.75}$ /day gained 4.5 kg in liveweight while apparently losing 5.5 kg in tissue weight. This discrepancy may have been due to a large gain in digesta mass since this was not included in CT-estimated whole body weight but would have been a component of liveweight. However, surprisingly, the difference between CT - estimated whole body weight and liveweight was inversely related to intake which would not be expected if this was an increased gut fill effect (Table 5.4).

To further investigate this discrepancy, data collected from 10 deer slaughtered at the conclusion of the experiment for which empty gut tissue weight was available was used in an attempt to account for the large apparent change in gut fill.

Table 5.2 *The initial, final and change in liveweight and individual tissue weight and respective energy retention rates for red and hybrid deer (n = 2) in winter.*

	Red deer							Hybrid deer						
ME intake (MJ ME/W $^{0.75}$/day)	0.44	0.49	0.53	0.57	0.64	0.73	*Ad lib*	0.42	0.49	0.53	0.56	0.64	0.70	*Ad lib*
Initial														
Initial Lwt (kg)	55.3	58.3	59.3	60.3	57.3	625	58.5	72.5	68.3	67.5	68.5	68.5	68	68.3
SEM (kg)	*2.8*	*2.3*	*1.8*	*1.8*	*3.0*	*3.5*	*2.0*	*4.5*	*0.3*	*2.3*	*2.5*	*2.0*	*5.5*	*3.0*
Adipose (kg)	1.96	1.90	2.06	1.85	2.13	1.81	1.99	2.24	1.72	2.06	1.63	1.64	1.41	1.97
SEM (kg)	*0.13*	*0.13*	*0.07*	*0.17*	*0.32*	*0.39*	*0.52*	*0.86*	*0.20*	*0.71*	*0.05*	*0.41*	*0.03*	*0.45*
Lean (kg)	32.24	33.66	35.70	35.18	34.65	35.66	32.64	41.04	39.80	39.53	38.09	40.09	37.71	40.24
SEM (kg)	*2.55*	*0.30*	*0.62*	*2.17*	*1.38*	*2.99*	*0.27*	*4.73*	*2.83*	*0.60*	*0.96*	*2.35*	*1.25*	*3.17*
Bone (kg)	7.36	7.50	7.17	7.01	7.08	7.28	7.12	9.04	8.82	9.22	8.85	8.97	8.28	8.50
SEM (kg)	*0.67*	*0.46*	*0.16*	*0.39*	*0.12*	*0.49*	*0.04*	*1.06*	*0.60*	*0.02*	*0.32*	*0.77*	*0.34*	*0.28*
GIT fat (g)	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.17	0.16	0.16	0.16	0.16	0.16	0.16
GIT protein (g)	390	400	410	410	410	410	400	450	440	440	440	440	440	430
Final														
Final Lwt (kg)	59.3	61.3	64.5	63.8	64.8	69.3	68.5	72.0	70.0	72.5	74.0	73.0	80.3	72.8
SEM (kg)	*5.3*	*0.3*	*0.0*	*1.3*	*3.8*	*4.8*	*1.5*	*1.3*	*3.8*	*2.8*	*1.5*	*8.3*	*2.8*	*0.5*
Adipose (kg)	1.57	1.52	1.71	1.89	2.09	2.50	2.76	1.79	1.35	1.72	2.00	2.05	2.05	3.00
SEM (kg)	*0.29*	*0.17*	*0.05*	*0.10*	*0.11*	*0.49*	*0.16*	*0.21*	*0.03*	*0.18*	*0.00*	*0.27*	*0.30*	*0.48*
Lean (kg)	34.49	34.19	36.08	36.97	36.34	39.49	37.97	41.86	40.39	41.33	41.32	41.44	40.19	47.31
SEM (kg)	*4.04*	*0.25*	*0.56*	*0.60*	*2.80*	*3.03*	*0.61*	*2.45*	*2.25*	*0.29*	*1.67*	*1.73*	*0.64*	*4.77*
Bone (kg)	7.39	7.54	6.92	7.28	7.42	7.72	7.99	9.74	9.37	9.04	9.26	9.12	8.79	9.30
SEM (kg)	*1.16*	*0.33*	*0.15*	*0.21*	*0.59*	*0.46*	*0.40*	*0.03*	*0.35*	*0.46*	*0.35*	*0.81*	*0.03*	*0.77*
GIT fat (kg)	0.15	0.15	0.15	0.15	0.16	0.16	0.17	0.17	0.16	0.17	0.17	0.17	0.18	0.17
GIT protein (g)	0.4	0.4	0.41	0.42	0.42	0.44	0.43	0.46	0.45	0.45	0.45	0.45	0.49	0.45
Change														
Adipose (g/day)	-8	-8	-7	1	-1	14	16	-9	-8	-7	8	8	13	21
Lean (g/day)	46	11	8	37	34	78	109	17	12	37	66	27	51	144
Bone (g/day)	1	1	-5	6	7	9	18	14	11	-4	8	3	10	16
Fat (g/day)	-4.6	-5.1	-5.5	1.9	1.1	12.4	15.2	-4.0	-3.4	-4.6	7.5	6.7	11.4	19.3
Protein (g/day)	11.2	2.5	0.4	10.4	10.1	22.1	31.8	7.0	5.2	7.9	18.6	7.9	15.5	40.4
E retention (kJ/day)	83	-140	-207	321	281	1009	1345	8	-12	5	731	452	816	1711
E retention (kJ/W $^{0.75}$/day)	3	-8	-12	19	15	56	77	3	0	0	38	24	44	84

Table 5.3 *The initial, final and change in liveweight and individual tissue weight and respective energy retention rates for red and hybrid deer (n = 2) in spring.*

	Red deer							Hybrid deer						
ME intake (MJ ME/W $^{0.75}$/day)	0.44	0.49	0.54	0.59	0.64	0.79	*Ad lib*	0.42	0.49	0.54	0.59	0.64	0.79	*Ad lib*
Initial														
Initial Lwt (kg)	74.0	72.8	71.8	69.8	69.5	65.5	72.0	79.3	75.8	82.8	74.0	90.3	77.3	79.3
SEM (kg)	*0.5*	*2.3*	*0.8*	*2.3*	*3.5*	*6.0*	*0.0*	*1.8*	*4.8*	*4.3*	*3.0*	*6.3*	*2.8*	*3.3*
Adipose (kg)	1.84	1.73	1.57	1.46	1.79	1.43	1.66	1.95	1.92	1.89	1.71	2.20	1.89	1.72
SEM (kg)	*0.07*	*0.23*	*0.05*	*0.00*	*0.25*	*0.06*	*0.13*	*0.05*	*0.04*	*0.05*	*0.09*	*0.01*	*0.14*	*0.21*
Lean (kg)	42.81	44.03	40.26	38.78	38.46	36.90	42.05	44.47	43.23	48.39	43.64	51.47	43.62	43.45
SEM (kg)	*0.58*	*4.49*	*0.72*	*1.63*	*0.18*	*3.78*	*0.70*	*0.70*	*3.51*	*3.99*	*0.38*	*4.27*	*2.58*	*1.30*
Bone (kg)	8.71	8.41	8.38	8.56	8.13	7.52	8.36	10.48	9.44	10.17	9.68	10.99	9.36	9.52
SEM (kg)	*0.65*	*0.60*	*0.49*	*0.28*	*0.33*	*1.07*	*0.21*	*0.59*	*0.43*	*0.71*	*0.84*	*0.28*	*0.33*	*0.66*
GIT fat (g)	0.17	0.17	0.16	0.16	0.16	0.15	0.17	0.18	0.17	0.18	0.17	0.19	0.17	0.17
GIT protein (g)	0.46	0.46	0.44	0.43	0.43	0.42	0.45	0.48	0.46	0.49	0.47	0.52	0.47	0.46
Final														
Final Lwt (kg)	78.5	77.3	75.8	78.8	79.0	76.8	90.0	78.5	76.5	83.0	82.5	103.8	92.0	98.8
SEM (kg)	*0.0*	*3.8*	*2.3*	*4.8*	*3.0*	*5.8*	*1.0*	*4.5*	*4.0*	*5.5*	*4.0*	*5.3*	*3.0*	*0.8*
Adipose (kg)	1.68	1.36	1.60	1.46	1.72	1.92	5.05	1.75	1.67	1.73	1.56	2.52	2.02	4.72
SEM (kg)	*0.20*	*0.03*	*0.01*	*0.11*	*0.04*	*0.30*	*0.21*	*0.19*	*0.08*	*0.04*	*0.12*	*0.41*	*0.08*	*0.14*
Lean (kg)	38.01	39.05	36.95	35.95	41.04	41.83	53.15	37.38	38.62	42.06	45.15	54.99	50.33	57.63
SEM (kg)	*0.58*	*2.08*	*0.42*	*5.36*	*0.53*	*3.88*	*0.73*	*4.06*	*1.51*	*1.64*	*2.35*	*3.29*	*1.63*	*2.43*
Bone (kg)	9.18	8.30	8.72	8.55	8.25	8.40	9.86	10.32	10.01	10.73	10.14	11.40	10.36	11.27
SEM (kg)	*0.76*	*0.42*	*0.57*	*0.61*	*0.28*	*0.52*	*0.03*	*0.05*	*0.23*	*0.62*	*0.13*	*0.14*	*0.01*	*0.52*
GIT fat (kg)	0.16	0.16	0.16	0.15	0.16	0.17	0.20	0.16	0.16	0.17	0.18	0.20	0.19	0.21
GIT protein (g)	0.43	0.43	0.42	0.42	0.44	0.45	0.54	0.44	0.44	0.46	0.48	0.54	0.51	0.56
Change														
Adipose (g/day)	-3	-8	1	0	-1	10	69	-4	-5	-3	-3	6	3	61
Lean (g/day)	-98	-102	-68	-58	53	100	227	-145	-94	-129	31	72	137	289
Bone (g/day)	10	-2	7	0	2	18	31	-3	12	11	9	8	20	36
Fat (g/day)	-2.5	-7.3	0.2	-1.0	0.3	11.2	55.9	-5.8	-3.4	-2.9	-0.2	6.8	6.9	52.2
Protein (g/day)	-22.2	-26.1	-15.1	-14.4	13.5	29.5	66.3	-36.9	-20.8	-29.5	9.7	20.0	38.8	82.7
E retention (kJ/day)	-622	-902	-349	-379	331	1136	3761	-1099	-626	-811	221	740	1187	4004
E retention (kJ/W $^{0.75}$/day)	-33	-45	-19	-23	18	62	174	-57	-31	-38	11	32	56	177

Table 5.4 *The initial, final and change in liveweight (kg), CT estimated liveweight (kg), whole body, carcass weight (kg), gut tissue and digesta weight (kg) for red and hybrid deer during spring.*

Genotype	Red					Hybrid				
Feeding level (g/kg $LW^{0.75}$/d)	41.7	45.8	54.2	66.7	*Ad. lib.*	41.7	45.8	54.2	66.7	*Ad. lib.*
Initial weight										
Liveweight (kg)	75.5	69.0	66.0	67.5	75.0	71.0	76.0	85.5	80.5	82.5
CT liveweight (kg)	66.4	58.1	58.8	58.0	62.1	59.4	64.3	71.9	69.7	67.0
CT whole body wt (kg)	59.4	51.4	47.9	50.7	50.1	50.6	50.3	60.1	57.7	56.8
CT carcass wt (kg)	52.6	46.2	43.4	44.3	45.2	45.4	50.3	54.1	51.7	51.3
Gut + digesta wt	7.0	6.7	10.9	7.3	11.1	8.8	8.6	11.8	12.1	10.2
Final weight										
Liveweight (kg)	78.0	72.5	74.0	82.5	89.5	70.0	79.5	96.5	95.0	101.5
CT liveweight (kg)	68.8	62.5	63.8	72.7	73.8	61.1	69.1	85.0	80.6	84.0
CT whole body wt (kg)	50.3	48.2	51.2	56.8	69.0	51.5	52.3	65.1	64.4	76.7
CT carcass wt (kg)	45.1	43.8	45.9	50.5	61.4	46.0	46.8	57.5	57.5	68.4
Gut + digesta wt (kg)	18.5	14.3	12.6	15.9	4.8	9.6	16.8	19.9	16.2	7.3
Gut tissue wt (kg)	2.95	2.90	2.18	3.56	3.86	2.75	3.27	3.99	3.97	4.21
Digesta (kg)	15.55	11.40	10.42	12.34	0.94	6.85	13.53	15.91	12.23	3.09
Weight change										
Liveweight (kg)	2.5	3.5	8.0	15.0	14.5	-1.0	3.5	11.0	14.5	19.0
CT Liveweight (kg)	2.4	4.4	5.0	14.7	11.7	1.7	4.8	13.1	10.9	17.0
CT Whole body weight (kg)	-9.1	-3.2	3.2	6.1	18.0	0.9	-3.4	5.0	6.8	19.8
CT carcass weight (kg)	-7.5	-2.4	2.5	6.2	16.2	0.6	-3.5	3.4	5.8	17.1
Apparent gut + digesta (kg)	11.5	7.6	1.7	8.6	-6.3	0.8	8.2	8.1	4.1	-2.9

where
liveweight = liveweight before scanning
CT liveweight = liveweight determined from refined CT images including GIT and digesta
CT whole body wt = weight determined from whole body CT images (excluding GIT and digesta)
CT carcass weight = weight determined from carcass CT images (all viscera excluding kidneys removed)
Gut + digesta weight = difference between CT liveweight and CT whole body
Gut tissue = fresh weight of GIT recorded after slaughter
Digesta = difference between gut + digesta weight and gut tissue
Apparent gut + digesta = difference between CT liveweight change and whole body wt (CT) change.

CT liveweight was calculated using refined images (which contained digesta). CT estimates of liveweight were consistently lower (14.5%) than liveweight recorded immediately prior to scanning. (Figure 5.3) but were highly correlated (0.92).

An estimate of full GIT weight was calculated by subtracting CT whole body weight from CT liveweight. Gut tissue weight collected at slaughter was used to calculate the mass of digesta in final CT liveweight. Gut tissue weight was subtracted from gut tissue + digesta weight to estimate digesta weight. Estimates of full GIT ranged from 7.0 to 12.3 kg for initial liveweight and 4.8 to 19.9 kg for final weight and generally increased with intake. Apparent weight of digesta (gut + digesta weight – gut tissue weight) appeared to decrease with increasing intake although the relationship was not strong.

Generally small liveweight gain at low intake was associated with large tissue loss and therefore presumably significant increases in gut fill and gut tissue weight. Increasing intake, increased liveweight gain, increased whole body weight and reduced the apparent increase in gut and digesta weight. Carcass weight and CT carcass weight were well correlated.

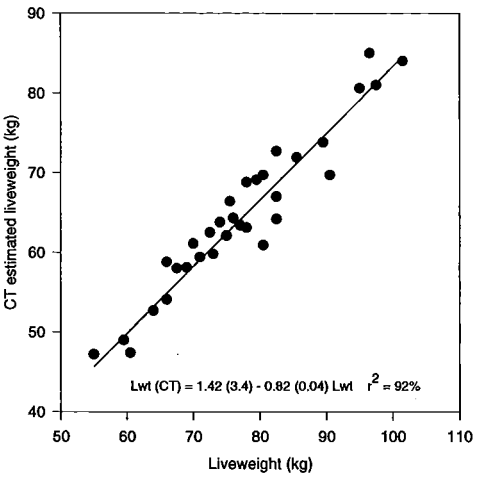


Figure 5.3. *The relationship between liveweight recorded immediately prior to CT scanning and liveweight estimated from CT images of whole body including GIT and its contents for deer (including those slaughtered) over a range of liveweight.*

Relative growth of tissues

Huxley's (1924) allometric growth equation $log\ Y = Log\ a + b\ log\ X$ was used to describe the relationship between individual tissue components of whole body and whole body weight. Relative growth curves for winter and summer are presented in Figures 5.4 and 5.5, respectively and the coefficients of the relationships in Table 5.5.

There was no significant difference ($P > 0.05$) between red and hybrid deer in growth coefficients for lean, bone or adipose tissue in whole body. However, there was a trend for hybrids to have a higher winter and a lower spring growth coefficient for fat compared with red deer. The average across-genotype growth coefficients were 0.991, 0.750 and 2.22 for lean, bone and adipose tissues respectively in winter. Spring values were 1.05, 0.486 and 2.00 for lean, bone and adipose tissues respectively (Table 5.6).

Table 5.5. *Linear regression equations describing the relationship between log whole body and log tissue weight (Figures 5.4 and 5.5) for red and hybrid deer in winter and spring.*

Season	Tissue	Genotype	Coefficient (b)	Constant	R^2	Slope	Elevation
Winter	Lean	Red	1.009	-0.117	0.97	NS	NS
		Hybrid	0.972	-0.055	0.99		
	Bone	Red	0.771	-0.407	0.61	NS	* *
		Hybrid	0.728	-0.293	0.66		
	Adipose	Red	1.697	-2.511	0.39	NS	* *
		Hybrid	2.737	-4.422	0.67		
Spring	Lean	Red	1.010	-0.115	0.98	NS	* *
		Hybrid	1.094	-0.269	0.98		
	Bone	Red	0.545	-0.001	0.48	NS	* *
		Hybrid	0.427	0.259	0.45		
	Adipose	Red	2.358	-3.777	0.71	NS	*
		Hybrid	1.638	-2.589	0.52		

Although the relative growth rate of tissues was not different between genotypes, red and hybrid deer did differ in their body composition at a common whole body weight as indicated by the significant elevation statistic. For both winter and spring, red deer had more adipose and less bone at the same whole body weight compared with hybrids. At the same body weight, lean tissue content was not significantly different between genotypes in the winter but red deer had slightly more lean tissue than hybrids in spring.

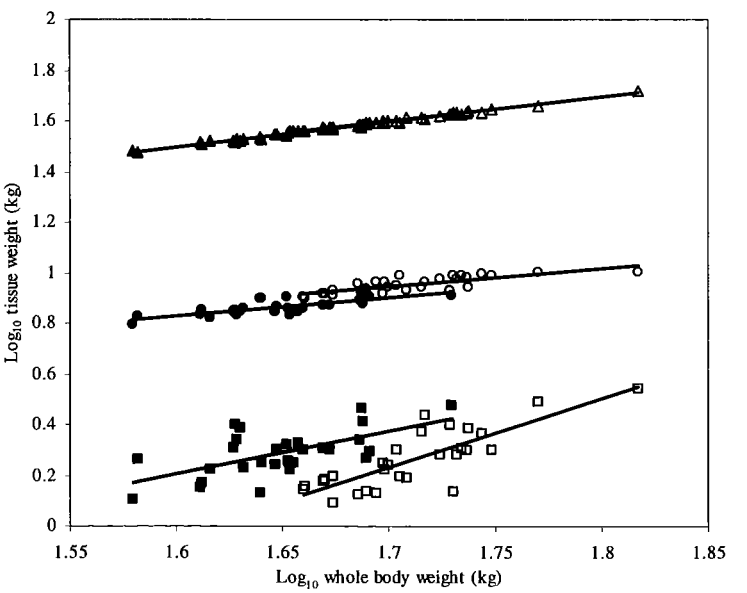


Figure 5.4. *Relative growth of lean (▲), bone (●) and adipose (■) tissue relative to whole body weight in red (solid symbols) and hybrid (open symbols) deer during winter.*

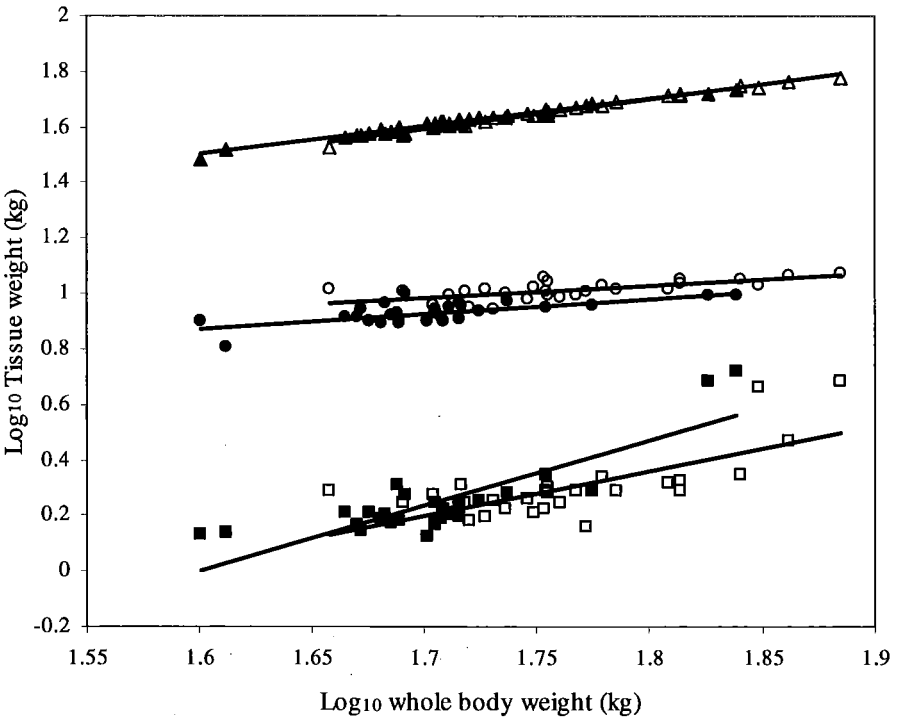


Figure 5.5. *Relative growth of lean (▲), bone (●) and adipose (■) tissue relative to whole body weight in red (solid symbols) and hybrid (open symbols) deer during spring.*

Although there were small non-significant differences between genotypes in relative growth of tissues, there was a significant effect of season on relative growth (Figure 5.6, Table 5.6).

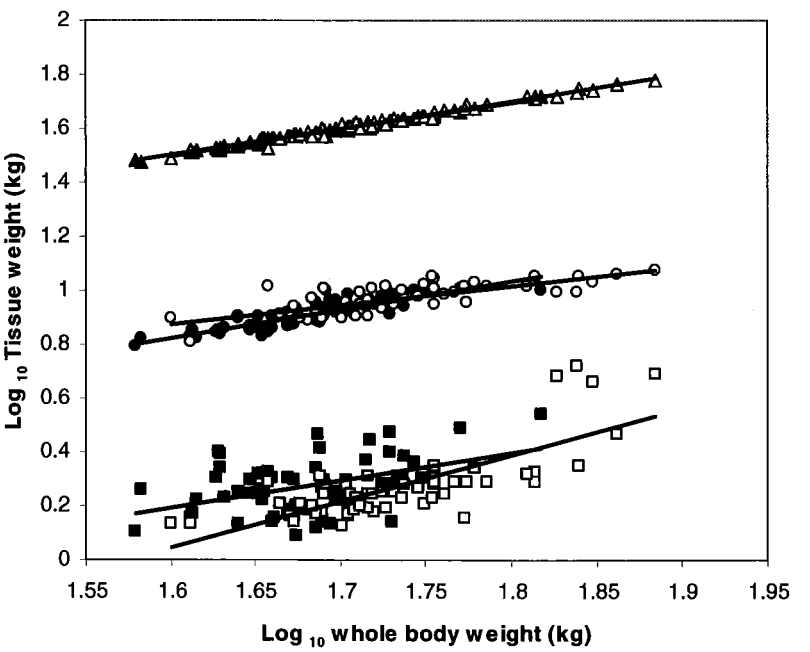


Figure 5.6. *Relative growth of lean (▲), bone(●) and adipose (■) tissue relative to whole body weight in winter (solid symbols) and spring (open symbols) for red and hybrid deer combined.*

In winter, bone grew relatively faster (1.06 vs 0.71) and adipose relatively slower (1.03 vs 1.73) than in spring. There was no seasonal difference in lean weight gain ($P > 0.05$).

Table 5.6. *Linear regression equations describing the relationship between log whole body weight and log tissue weight (Figure 5.6) for red and hybrid deer combined in winter and spring.*

Tissue	Season	Coefficient (b)	Constant	R^2	Slope	Elevation
Lean	Winter	0.983	-0.075	0.99	NS	NS
	Spring	1.020	-0.136	0.98		
Bone	Winter	1.063	-0.873	0.80	* *	NS
	Spring	0.708	-0.258	0.58		
Adipose	Winter	1.026	-1.448	0.21	* *	* *
	Spring	1.727	-2.723	0.59		

It is apparent from Figure 5.6 that at the same whole body weight, deer in spring had less adipose than in winter. Figure 5.7 presents relative adipose growth based on measurements made at the end of the winter and beginning of spring experimental periods

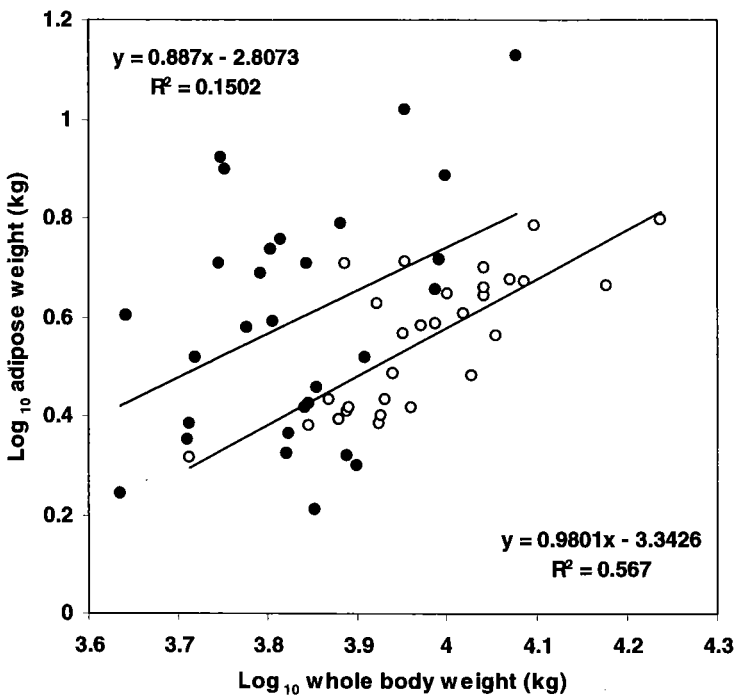


Figure 5.7. *Relative growth of adipose tissue based on data collected at the end of the winter (●) and beginning of the spring (O) experimental periods.*

Dressing out %

The dressing out percentage (DO %) was calculated for 10 deer (5 red deer and 5 hybrids) when slaughtered at the conclusion of the spring trial in mid December (12 months of age). The slaughter group was selected in order that in each nutritional level chosen both genotypes were represented. DO % was defined as;

$$DO\% = \frac{\text{hot carcass weight (kg)}}{\text{pre-slaughter liveweight (kg)}} \times 100$$

There was no significant effect of genotype. Red deer dressed out at on average 57.5 ± 1.3% and hybrids at 56.9 ± 1.1% (mean ± SEM).

The DO % of all deer was estimated by predicting hot carcass weight from CT carcass weight (Figure 5.8) derived from the 10 slaughtered deer. The relationship between CT carcass weight and hot carcass weight for these deer was not significantly different between genotypes and therefore a common equation was used. Estimated DO % using hot carcass weight predicted from CT carcass weight was not significantly different between red deer (53.1 ± 1.4 %) and hybrids (55.7 ± 1.0 %)

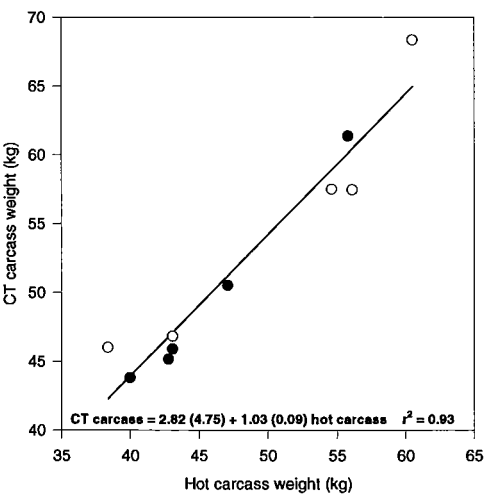


Figure 5.8. *The relationship between hot carcass weight and CT derived carcass weight for red deer (●) and hybrids (O) slaughtered at approximately 12 months of age.*

5.3 Discussion

CT analysis methods

Conclusions drawn about body composition and energy metabolism (Chapter 5b) from this work rely entirely on the ability to accurately estimate the weight of adipose, lean and bone tissues. There was evidence this was achieved with the use of CT techniques.

CT liveweight and changes in CT liveweight were well correlated with pre-scan actual liveweight and changes in pre-scan actual liveweight although CT liveweight was consistently lower (approximately 15%) than pre-scan liveweight (Figure 5.3). The difference between liveweight and CT liveweight was probably due to the exclusion of the head and part of the upper neck from CT liveweight. Previous estimates (Early *et al.,* 1990) based on cattle data indicate the head was approximately 10% of carcass weight. Based on a dressing out percentage of 58 %, this translates to the head being about 6 % of liveweight for weaner deer. Inclusion of the upper part of the neck, hocks and muddied pelage is likely to reconcile the remaining differences between liveweight and CT liveweight.

Carcass weight estimated using carcass images (CT carcass weight) was 2.8 kg heavier than hot carcass weight measured after slaughter (Figure 5.8) but was well correlated. The fact that liveweight and CT liveweight (Figure 5.3), liveweight change and CT liveweight change (Table 5.4) and carcass weight and CT carcass weight (Figure 5.8) were strongly correlated is good evidence that the scanning procedure in conjunction with tissue volume to tissue weight conversion factors provided reliable estimates of individual tissue weights.

However, changes in CT whole body weight were not well correlated with changes in liveweight or CT liveweight. For example, in some cases liveweight increased by 2.5 kg but CT whole body weight apparently decreased by 9 kg. There was no evidence that CT whole body weight should be determined any less accurately than either CT liveweight or CT carcass weights which were strongly correlated to their respective actual measurements. Therefore, because the only difference between CT liveweight and CT whole body weight was gut + digesta weight, changes in gut fill and gut weight must, by definition explain the discrepancy. This implies there were large changes in gut weight and gut fill which were negatively correlated with intake. Further evidence that this was a real effect was that changes in CT carcass weight mirrored the apparent changes in CT whole body weight and at the same time were well correlated with hot carcass weight. There was also a positive relationship between CT liveweight and CT whole body weight at the beginning of spring. While these apparent changes in gut and digesta weight were not anticipated, there is strong evidence from liveweight and carcass weight that CT measurements accurately measured tissue weights and

therefore gut changes were a real effect. In light of this, whole body weight and the weight of individual tissues were used for analysis with a degree of confidence.

There would be a greater degree of confidence in whole body weight measurements if a plausible explanation for the apparent changes in gut fill existed. There are two possible explanations for the apparent increase in gut fill when intake is restricted. Either deer on restricted diets may have (1) eaten considerable amounts of bedding (sawdust) or (2) retained large amounts of water compared with deer on high intakes.
It is unlikely that wood shavings were a significant proportion of the diet for 2 reasons. Firstly, each pen was lined with only about 2-3 kg of shavings which, initially, deer showed little interest in and there was no visually detectable disappearance over the three days before bedding was removed and replaced. Secondly, shavings were spread over the pen floor and became quickly soiled rendering them unpalatable to deer.

Increases in water consumption might well explain differences in gut fill, although water intake was not measured. Previous authors (D. Freudenburger *pers. com*) have noted increased water intake of animals with reduced DM intake and have hypothesised that it might be a way of deer achieving some sort of satiety. A difference in gut fill, which was negatively correlated with intake would have occurred if, after the beginning of the experiment restricted animals began consuming greater quantities of water than they had previously which subsequently was retained in the gut.

Techniques for removing digesta

In comparative slaughter experiments, digesta is removed from the gastrointestinal tract before whole body composition is estimated and the same would be desirable when using CT images to estimate body composition. However, when determining body composition based on CT scans, removal of digesta from images presents problems. Removal of all digesta from the rumen and folds of the GIT is a sisyphean task and dramatically increases image processing time. In addition, identification of the digesta-GIT tissue boundary is difficult especially posterior of the stomach and attempting the removal of digesta would increases the likelihood of errors associated with removing GIT tissue or leaving digesta.

There are four other options to deal with digesta in whole body images. (1) Leave all digesta in images (2) remove total GIT including digesta (3) remove only significant areas of digesta or (4) remove all digesta and GIT as in (1) but add back to whole body weight an estimate of GIT weight (as done in this experiment).

Compared with removing all digesta, leaving digesta in whole body images has the advantage of avoiding the problem of distinguishing the digesta-GIT tissue boundary and accurately removing digesta from images in addition to speeding up image processing time. However, inclusion of digesta in whole body images would lead to an overestimation of whole body weight and a poor estimation of composition. Removing both GIT and digesta, while eliminating the need to distinguish the digesta-GIT tissue interface, would under estimate whole body weight. The relative proportion of GIT tissue and digesta within the GIT would dictate which of options 1 and 2 would cause the smallest error in whole body weight.

The weight of the empty GIT of the 14 deer slaughtered at the conclusion of the trial was compared to the total weight of intestines (GIT plus digesta) as estimated from the CT images for those deer before slaughter. On average GIT tissue was 44 ± 3.8% of the total full intestine weight. Sibbald and Milne, (1993) calculated a figure of 30% in deer on a similar concentrate diet with additional hay. Therefore, the majority of full GIT weight (GIT + digesta) appears to be digesta. By including digesta in whole body weight, the amount by which tissue weight has the potential to be over estimated is greater than the amount by which tissue weight would have been underestimated as a result of removing total gastrointestinal tract. On this point alone, it would appear removal of all GIT to ensure total digesta removal would be advantageous compared to complete inclusion. Furthermore, the relative density of digesta was such that a significant proportion would have been recorded as adipose.

This is illustrated in Plate 5.4 where an abdominal image containing a digesta-filled rumen has had the pixels associated with adipose (35 - 121 grey scale) highlighted in yellow.

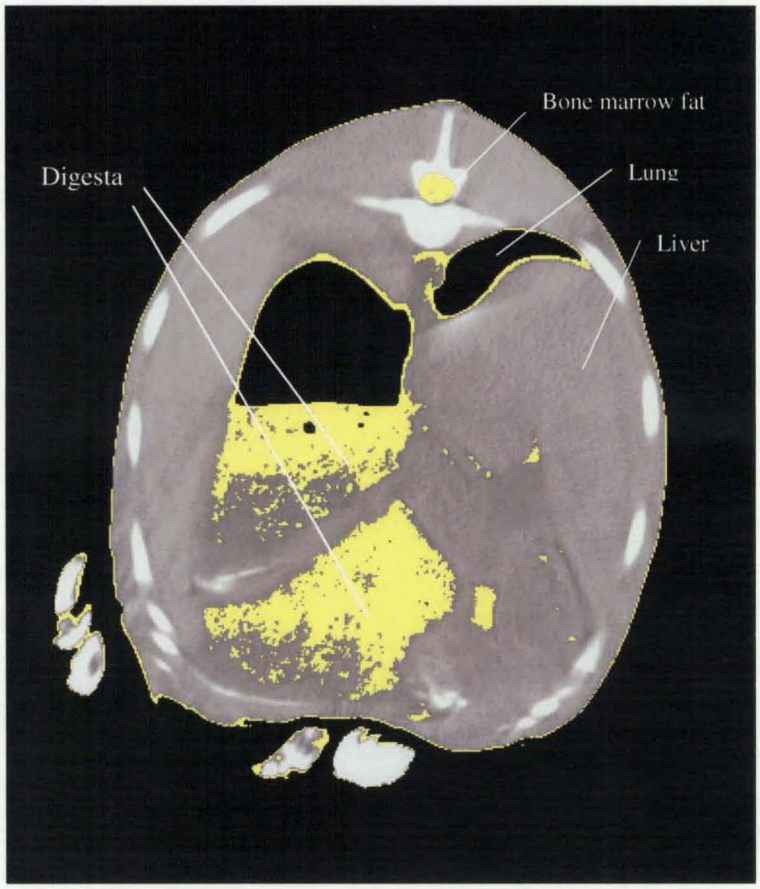


Plate 5.4. *A CT image in the abdominal region of a deer with the pixels in the grey scale range associated with adipose highlighted in yellow.*

In terms of total body energy, including digesta could significantly overestimate whole body energy and presumably more so for animals with a greater gut fill. Analysis of images containing digesta indicates that for every 1 kg of digesta remaining in intestines, total body energy would have been overestimated by 7 %. An error of 7 % would be significant in relation to the 13 % difference in total body energy recorded between red deer and hybrids at the conclusion of the spring experiment.

Previous authors (N. Jopson, J.Thompson *pers com.*) have adopted a policy of removing only areas of digesta in the rumen and significant areas of digesta in the intestines (bigger than half the size of the kidney). Removing significant areas of digesta reduces the effect of having digesta in whole body as described above but does not completely remove it. This approach does not avoid the problem of identifying the digesta-GIT tissue boundary, requires the operator to make a subjective assessment of digesta area size on which to base a decision on whether to remove or leave digesta introducing a further source of error, and places some restriction on image processing speed.

An alternative option, was to remove both GIT and digesta from images as in option (2) but to add back to whole body weight an estimate of empty GIT tissue weight. Complete removal of GIT and digesta would not only increase the speed and ease of digesta removal from images but would

eliminate subjective assessment of digesta area and the need to identify the digesta-GIT tissue boundary.

Data from this study suggest the weight of gastrointestinal tract can be reliably (SE = 0.2 kg) predicted from CT estimated GIT-free body weight (Figure 5.2). (Jagusch *et al.*, 1970) provided values for the composition of GIT which allow an estimate of empty GIT energy. The empty GIT energy was added to the gastrointestinal tract free estimates of body energy to provide a more complete estimate of total body energy.

Composition of gain – effect of genotype

There was a clear trend for red deer to deposit a greater amount of adipose in spring and less in winter compared with their hybrid counterpart. (Table 5.5) but the genotype difference did not reach significance. The small number of deer at each feeding level and the experimental design which allocated a disproportionate number of deer to low intake to enable a better ME_m estimation may have prevented this difference being statistically significant. However the trend for red deer to deposit a greater amount of adipose in spring and less in winter compared with their hybrid counterpart is consistent with the trends in liveweight gain in Chapter 4a and with the energy costs of gain (See Chapter 5b).

Composition of gain – effect of season

This is the first experiment to show significant winter-spring differences in the relative growth of fat and bone tissue in young deer. In winter, bone grew relatively faster and adipose relatively slower than in spring. Results from previous studies have suggested that, in young lambs (Forbes *et al.*, 1979; Forbes *et al.*, 1981) and steers (Philips *et al.*, 1997), long day length stimulated the growth of non-fat tissues at the expense of fat.

Of particular note was the relatively large loss of total adipose from stags in early spring (Figure 5.7) At the same body weight stags in October had relatively less adipose tissue as they had in mid-August. Unfortunately, during this period, deer were released onto pasture and consequently moved from a concentrate to a pasture-dominant diet and for many DM intake would have increased. It is unclear whether the loss of adipose tissue relative to whole body weight which occurred over this period was a result of these management related changes or reflect an intrinsic seasonal change in the composition of body weight gain.

Early spring represents a period of rapid growth for young stags and catabolism of fat reserves may represent a mechanism which allows stags to achieve a higher rate of liveweight gain than on early spring pasture alone. As a consequence, deer which have been under nutritional stress and emerge from the winter low in body condition may not achieve as rapid liveweight gain as cohorts that are able to supplement early spring feed with energy from fat reserves. The effect of winter body condition on early spring growth needs further investigation.

In both seasons, the elevation term for relative growth equations were significantly different between genotypes. This indicated that while relative growth coefficients may be similar, at the same body weight, genotypes differed in whole body composition. For example, in both seasons red deer had proportionately less bone and more adipose tissue than hybrid deer at the same whole body weight. This difference was evident at the beginning of winter and suggests relative growth coefficients for adipose and bone tissue for red and hybrid deer must have been different during a previous stage of development. The lower relative adipose content of hybrid deer at 6 months of age compared with red deer may in part be responsible for the higher rate of liveweight gain exhibited by hybrids in their first 6 months of life.

Dressing out percentage

The estimates of DO % of yearling stags are similar to those of Drew and Hogg, (1990) who reported DO % of 1 year stags of 54.6 and 56.8 % for red deer and hybrids, respectively and similar to Soetrisno *et al.* (1994) of 52 - 56 %. These are higher than other domestic livestock (sheep cattle 40 - 50%). There was no evidence of differences between genotypes.

5.4 Conclusion

Results in Chapter 5a rely entirely on the ability to accurately predict body composition. While there was good agreement between liveweight and carcass weight and those measurements estimated by CT scanning changes in whole body weight relative to liveweight suggested large changes in gut fill that were not expected. Conclusions from Chapter 5a must be tempered in knowledge of this.

There was a trend for red deer to deposit more adipose in spring and less in summer than hybrids. This observation was consistent with the trends in liveweight gain seen in Chapter 5b. However, the greatest difference was between seasons. During winter, deer liveweight gain contained proportionately less adipose and more bone tissue than in spring. Stags appeared to lose relatively large amounts of adipose in early spring. This may help to explain in part the rapid spring liveweight gain achieved by deer.

Chapter 5b

Comparative energy metabolism of red deer *(Cervus elaphus)* and red x elk hybrids *(Cervus elaphus spp).*

5.0 Introduction

The experiment reported in Chapter 2a showed that red and hybrid deer offered feed *ad lib.* during winter had similar relative liveweight gain (g/kg $^{0.75}$/day) and intake (g DM/kg $^{0.75}$/day) During spring however, hybrids gained liveweight faster compared to red deer but had a similar relative intake. Although red deer appeared to have a lower ME requirement for liveweight maintenance (Chapter 2b) the value was low compared to other estimates (Fennessy *et al.*, 1981; Suttie *et al.*, 1987) and therefore required validation. It was also unclear whether the lower ME requirement for liveweight maintenance in red deer reflected a lower ME requirement at zero energy balance or alternatively that the composition and energy value of liveweight change was different between genotypes.

In addition to measuring the partial efficiency of metabolisable energy for energy gain, this study was designed to provide estimates of ME_m for zero energy balance and further estimates of ME_m for liveweight maintenance. To enable a more robust estimate of ME_m, feeding treatments were chosen so that a disproportionate number of deer were offered a ration closer to maintenance rather than *ad lib.*

5.1 Materials and methods

Data obtained in this experiment was from the same animals and concurrent to the measurements reported in Chapter 5a. The details of animals, feed and housing are presented in Chapter 5a.

Inter - conversions of tissues

Where the mass of fat and protein rather than adipose, lean and bone tissue was required, each tissue weight was multiplied by an estimate of the relative proportion of fat and protein in each tissue (Table 5.7). The relative proportions of fat and protein were determined by chemical analysis of duplicate samples of adipose and lean tissue collected from freshly slaughtered deer carcasses and from previous estimates (Mello *et al.*, 1978) for bone.

Table 5.7. *The proportion of fat, protein, water and ash (g/kg fresh) in samples of lean and adipose from freshly slaughtered deer carcasses and in bone based on the work of Mello et al. (1978).*

Component	Adipose	Lean	Bone
Water	263	719	320
Protein	44	247	231
Fat	692	17	139
Ash	<1	16	310

where water = weight lost by evaporation after oven drying at 90°C for 48 h
protein = standard Kjeldahl nitrogen x 6.25
fat = standard Soxhlet extraction
ash = residue after combustion at 550°C in muffle furnace for 8 h

The mass of body fat was calculated by multiplying adipose tissue mass by 0.692, lean by 0.017 and bone by 0.139 with the sum of the products being an estimate of total ether-extractable fat. For an estimate of crude protein mass, adipose tissue mass, lean tissue mass and bone mass were multiplied by 0.044, 0.248 and 0.232, respectively and summed. When reporting on body composition, the terms adipose, lean and bone were assigned to describe the animal tissue while the terms fat and protein were used, specifically, to describe the chemical nature of these tissues where fat was ether-extractable fat (standard Soxhlet extraction, Soxtec system HT1043 Extraction Unit, Tecator Sweden) and protein was defined as nitrogen content (standard Kjeldahl extraction, kjeltec Auto 1035 analyzer, Tectato Sweden) x 6.25.

The heat of combustion of fat and protein were assumed to be 39.3 and 23.6 MJ/kg DM for fat and protein respectively (ARC, 1980).

Statistical Analysis

Mean daily liveweight gain for individual animals was defined as the regression coefficient of the linear relationship between liveweight (kg) measured weekly and time (days) and expressed as grams/day. The relationships between intake and liveweight gain were fitted using linear or multiple regression. Differences in regression coefficients and intercept values between relationships for each genotype were tested using the method of Snedecor and Cochran (1980). Differences in *ad lib.* intake between genotypes and seasons were analysed using ANOVA.

5.2 Results

Feed intake

The DM intake and ME intake for pairs of red and hybrid deer are given in Table 5.8 for winter (a) and spring (b), respectively. During winter, *ad lib.* intake was not significantly different between genotypes ($P > 0.05$) when expressed on a metabolic liveweight basis and either genotype consumed on average 0.68 ± 0.03 MJ ME/W $^{0.75}$/day. Refusals averaged 28% and 23% of feed offered for *ad lib.* fed red and hybrid deer, respectively and indicated access to feed was not limited. During spring, mean *ad lib.* intake was about 30% higher than in winter and was greater for hybrid than for red deer. Mean spring *ad lib.* intake was 0.97 ± 0.02 MJ ME/W $^{0.75}$/day (mean ± SEM) and 1.05 ± 0.01 MJ ME/W $^{0.75}$/day (mean ± SEM) for red and hybrid deer, respectively. During spring, deer on restricted diets ate 100 % of the prescribed ration although during winter there were generally small amounts of refusals at all but the lowest allowance.

Table 5.8. *Dry matter and metabolisable energy intake of red and hybrid weaner stags offered varying amounts of a commercially pelleted diet[1] during the winter (a) and spring (b) (2 stags per genotype x feeding level, n=28).*

(a)

Feed offered (g/W $^{0.75}$ /day)	37.5		41.7		45.8		50.0		54.2		66.7		*Ad lib*	
Genotype	Red	Hybrid	Red	Hybrid	Red	Hybrid	Red	Hybrid	Red	Hybrid	Red	Hybrid	Red	Hybrid
Liveweight (kg)	60.7	72	60.4	70.8	62.9	70.8	62.5	70.6	61.3	71.2	65.6	75.2	62.8	70.6
DMI (g DM/day)	799	876	889	995	992	1099	1060	1158	1178	1322	1390	1577	1375	1523
DMI (g DM/W $^{0.75}$ /day)	36.7	35.4	41	40.8	44.4	45	47.7	47.5	53.8	53.9	60.3	61.8	61.6	62.5
MEI (MJ/day)[2]	9.3	10.2	10.4	11.6	11.6	12.9	12.4	13.5	13.8	15.5	16.3	18.5	16.1	17.8
MEI (MJ/W $^{0.75}$ /day)[2]	0.43	0.41	0.48	0.48	0.52	0.53	0.56	0.56	0.63	0.63	0.71	0.72	0.72	0.73

(b)

Feed offered (g/W $^{0.75}$ /day)	37.5		41.7		45.8		50.0		54.2		66.7		*Ad lib*	
Genotype	Red	Hybrid	Red	Hybrid	Red	Hybrid	Red	Hybrid	Red	Hybrid	Red	Hybrid	Red	Hybrid
Liveweight (kg)	75.6	77.8	73.8	75.5	73	82.9	75.5	79.5	74.5	96.1	71.4	85.7	83.2	89
DMI (g DM/day)	955	949	1062	1080	1158	1273	1293	1344	1389	1681	1656	1901	2435	2792
DMI (g DM/W $^{0.75}$ /day)	37.3	36.2	42.2	42.2	46.4	46.4	50.5	50.5	54.8	54.8	67.5	67.5	88.5	96.3
MEI (MJ/day)[2]	11.2	11.1	12.4	12.6	13.5	14.9	15.1	15.7	16.3	19.7	19.4	22.2	28.5	32.7
MEI (MJ/W $^{0.75}$ /day)[2]	0.44	0.42	0.49	0.49	0.54	0.54	0.59	0.59	0.64	0.64	0.79	0.79	1.04	1.13

Liveweight is the average liveweight recorded through the experimental period
DMI is daily dry matter intake
MEI is daily metabolisable energy intake
1. All-purpose ration (APR plus) Target Stock Feed, Arches Milling Company, Rangiora, NZ.
2. Calculated using ME value of 11.7 MJ ME/kg DM

Liveweight gain – effect of genotype

During winter, ME intake had a significant effect on liveweight gain (Figure 5.9). Liveweight gain of weaners during July and August increased from about 0 g/W $^{0.75}$/day to 10 g/W $^{0.75}$/day (220 g/day) over the range of intakes offered.

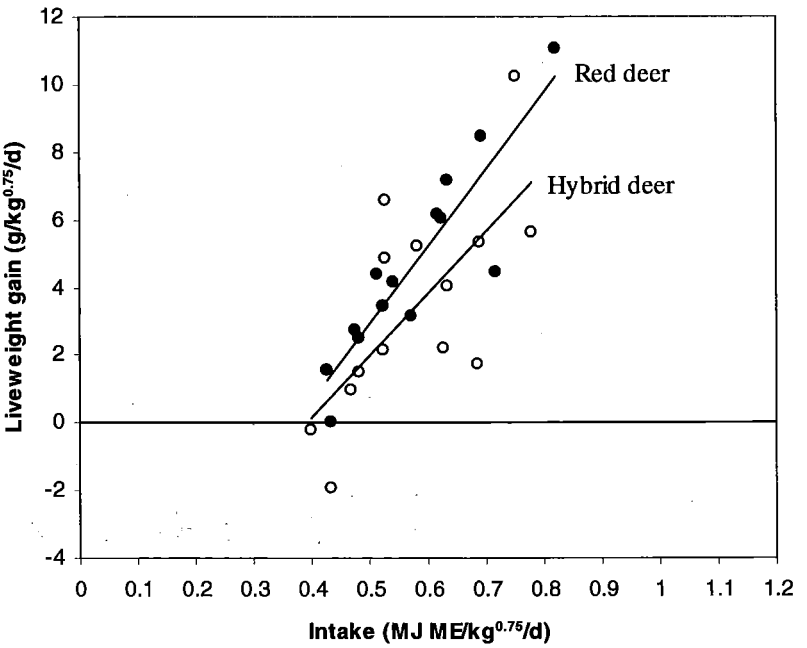


Figure 5.9. *The linear relationship between ME intake (MJ ME/W $^{0.75}$/day) and liveweight gain (g/W $^{0.75}$/day) of red (●) and hybrid deer (O) in winter.*

The linear relationship between ME intake (MJ ME/W $^{0.75}$/day) and liveweight gain (g/W $^{0.75}$/day) for both genotypes in winter was;

Red deer	LWG = -8.5 (1.9) + 22.8 (3.2) ME Intake	R^2 = 81%	n = 14
Hybrid deer	LWG = -7.3 (3.2) + 18.4 (5.5) ME Intake	R^2 = 48%	n = 14

There was no significant difference (P > 0.05) in slope (b) or intercept (c) values for the relationships. However, the linear relationships predicted that at *ad lib.* intake (0.73 MJ ME/W $^{0.75}$/day) red deer gained relative liveweight faster (8.1 g/W $^{0.75}$/day) than hybrids (6.1 g/W $^{0.75}$/day). Estimates of ME_m were 0.37 and 0.39 MJ ME/W $^{0.75}$/day for maintenance of liveweight and the estimates of the cost of liveweight gain were 44 and 55 MJ ME/kg liveweight gain for red and hybrid deer respectively, during winter. The trend of winter liveweight gain to be greater for red deer compared with hybrids at *ad lib.* intake was similar to the findings reported in Chapter 4.

The relationship between ME intake (MJ ME/W $^{0.75}$/day) and liveweight gain (g/W $^{0.75}$/day) for the combined data from both genotypes was;

LWG = -7.8 (1.9) + 20.5 (3.3) ME Intake R^2 = 60% n = 28

This relationship gives values of 0.38 MJ ME/W $^{0.75}$/day for maintenance of liveweight and 49 MJ ME/kg liveweight gain during winter.

Spring liveweight gain was best described by a non - linear relationship with intake (Figure 5.10) ranging from -0.5 g DM/W $^{0.75}$/day. (-130 g/day) to 18 g DM/W $^{0.75}$/day. (470 g/day). A second order polynomial curve was fitted to the data. The relationship between ME intake (MJ ME/W $^{0.75}$/day) and liveweight gain (g/W $^{0.75}$/day) for each genotype was;

Red LWG = -16.2 (10.4) + 55.7 (29.9) ME intake - 27.1 (20.1) ME intake ^{2} R^2 = 66% n=14
Hybrid LWG = -34.7 (7.6) + 94.3 (21.5) ME intake - 43.5 (14.3) ME intake ^{2} R^2 = 90% n=14

Estimates of liveweight maintenance requirements were 0.35 and 0.47 MJ ME/W $^{0.75}$/day for red and hybrid deer, respectively. When a linear relationship was fitted to spring data regression coefficients and intercept values were both significantly different ($P < 0.05$) and the energy cost of gain was 64 and 35 MJ ME/kg liveweight gain for red and hybrid deer, respectively. The trend for red deer to have a lower maintenance requirement but a higher cost of gain compared with hybrid stags was similar to the findings in Chapter 4.

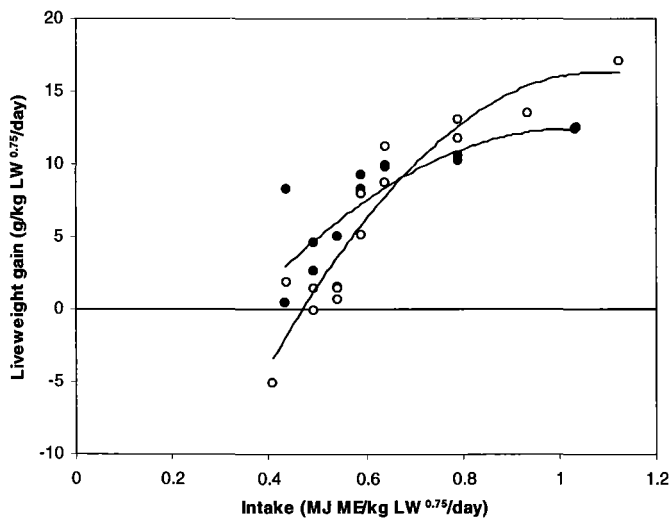


Figure 5.10. *Relationship between ME intake (MJ ME/W $^{0.75}$/day) and liveweight gain (g/W $^{0.75}$/day) of red (●) and hybrid deer (O) in spring.*

Liveweight gain – effect of season

There was no significant seasonal difference in ME_m for zero liveweight gain or the efficiency with which ME was used for liveweight gain (Figure 5.11).

The common relationship for both red and hybrid deer in winter and spring between ME intake (MJ ME/W $^{0.75}$/day) and liveweight gain (g/W $^{0.75}$/day) was;

LWG = 22.9 (2.2) ME intake - 8.5 (1.4) R^2 = 68% n = 56

Energy requirement for zero liveweight gain in both winter and spring was 0.37 MJME/W $^{0.75}$ /day and for liveweight gain 44 MJ ME/kg. The efficiency of utilisation of ME for liveweight gain was 0.23.

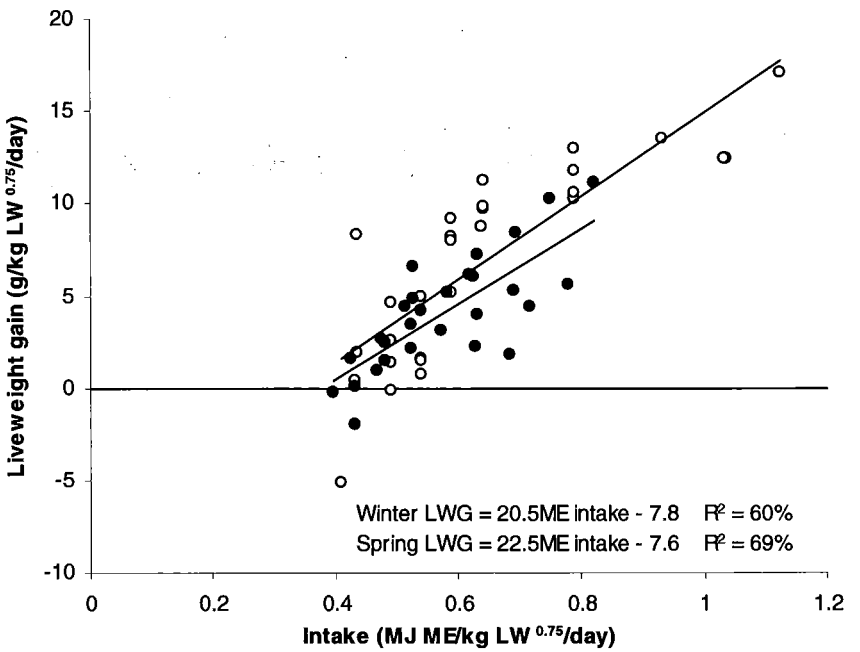


Figure 5.11 *Relationship between ME intake and liveweight gain in red and hybrid deer during winter (●) and spring (O).*

Whole body weight gain – effect of genotype

There appeared to be large changes in gut fill during this experiment (see chapter 5a) which would have been included in changes in liveweight. The response in whole body weight (as determined by CT measurements) to ME intake was investigated as an alternative to liveweight. The linear relationship between ME intake (MJ ME/W $^{0.75}$/day) and whole body gain (g/W $^{0.75}$/day) for both genotypes in winter was;

Red	WBG = 20.1 MEI - 8.7	n =14	R^2 = 49%
Hybrid	WBG = 19.5 MEI - 8.0	n = 14	R^2 = 45%

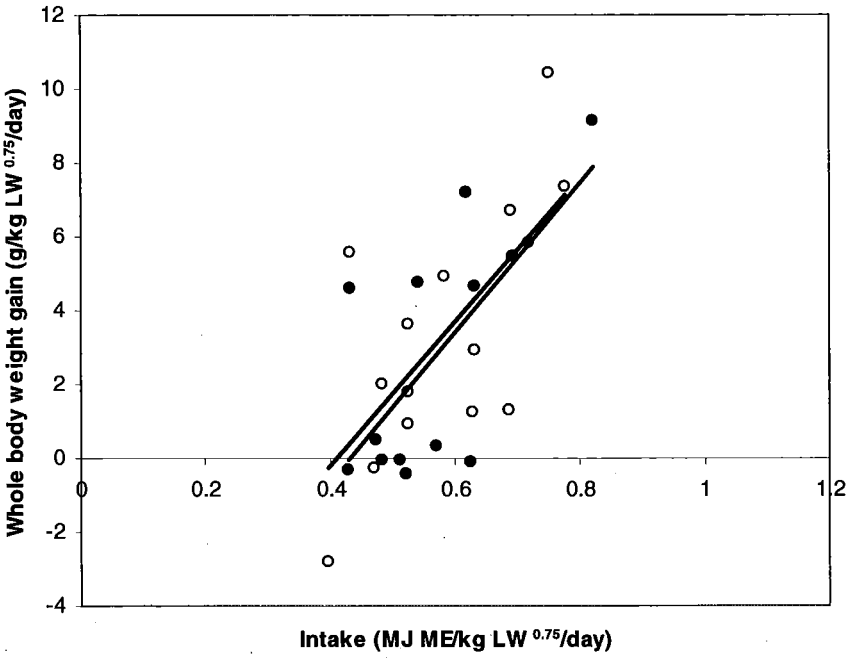


Figure 5.12. *Relationship between ME intake and whole body weight gain of red* (O) *and hybrid* (●) *deer during winter.*

There was no significant difference between genotypes in the relationship of whole body weight change to ME intake. Both genotypes required 0.42 MJ ME/W $^{0.75}$/day for maintenance and 50.9 MJ ME/kg of whole body gain.

The linear relationship between ME intake (MJ ME/W $^{0.75}$/day) and whole body gain (g/W $^{0.75}$ /day) for both genotypes in spring was;

Red	WBG = 36.6 MEI - 22.6	n = 14	R^2 = 85%
Hybrid	WBG = 40.1 MEI - 24.1	n = 14	R^2 = 83%

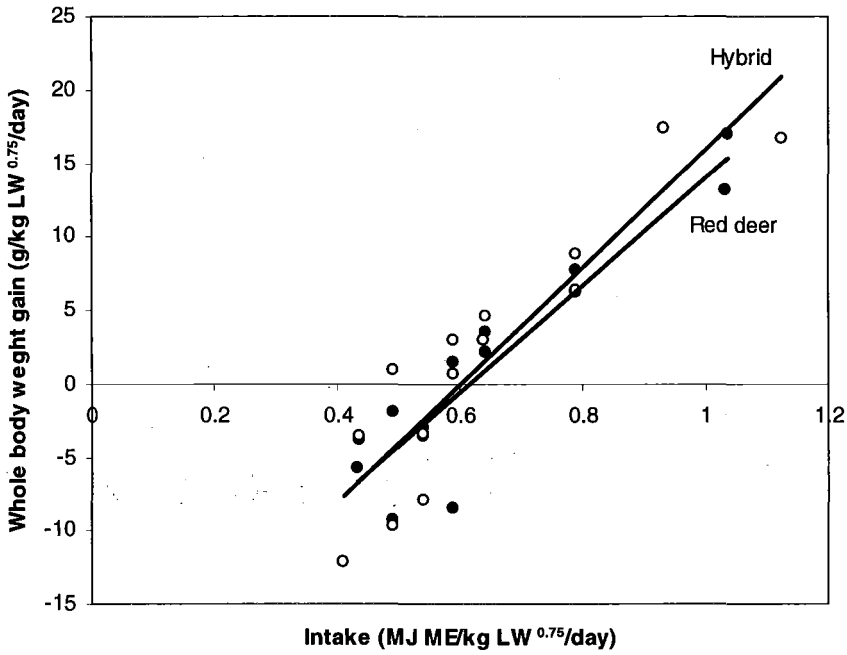


Figure 5.13. *Relationship between ME intake and whole body weight gain (g/kg W $^{0.75}$ /day) of red (O) and hybrid (●) deer during spring.*

There was no significant difference between genotypes in the response to whole body weight change to ME intake. Both genotypes required 0.61 MJ ME/W $^{0.75}$/day for maintenance and 26.7 MJ ME/kg of whole body gain.

Whole body weight gain –effect of season

There were significant seasonal differences in the energy requirement for zero whole body gain and the cost of whole body gain (Figure 5.14).

The seasonal relationship between ME intake (MJ ME/W $^{0.75}$ /day) and whole body gain (g/W $^{0.75}$ /day) was;

Winter	WBG = 19.8 MEI - 8.4	n=28	R^2 = 47 %
Spring	WBG = 38.4 MEI - 23.4	n= 28	R^2 = 83 %

Deer required 0.42 MJME/W $^{0.75}$ /day for zero whole body gain in winter and 0.61 MJME/W $^{0.75}$ /day in spring. Whole body weight gain cost 50.9 MJ ME/kg in winter and 26.7 MJ ME/kg in spring.

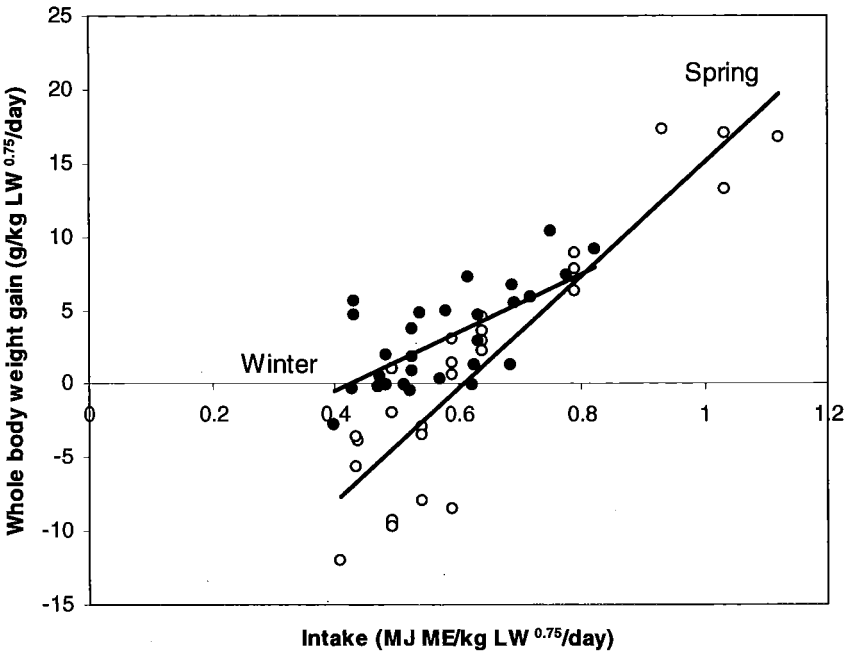


Figure 5.14. *Relationship between ME intake and whole body weight gain (g/kg $W^{0.75}$ /day) of deer in winter (●) and spring* (O).

Energy retention – effect of genotype

The relationship between ME intake and net energy retained in whole body during winter and spring is given in Figures 5.15 and 5.16, respectively. The relationships given include individuals with negative net energy retention values. It is conventional to remove individuals with negative net energy retention values from this type of analysis since the efficiency of utilisation of energy for maintenance (k_m) is greater than the efficiency of utilisation for energy gain (k_g). However, in this case, there are two reasons why negative net energy retention values were included.

The separate relationships for positive and negative values for red deer and hybrids in winter are given in Figure 5.15a. The ME requirement for zero energy balance derived from positive values was 0.24 MJ ME/$W^{0.75}$ /day but from negative values was 0.62 MJ ME/$W^{0.75}$ /day. Theoretically, estimates of ME_m should be the same regardless of whether they are calculated from individuals in positive or negative energy balance. On this basis, a common relationship was fitted to both positive and negative energy retention values which forced a common ME_m value.

In addition, it is difficult to justify the removal of individuals with only slightly negative net energy retention values when errors involved in CT analysis are considered. For example, a 5 % underestimation of whole body weight at the conclusion of the study would have caused an animal at zero energy balance to record a net energy loss of 20 kJ/kg $BW^{0.75}$/day. Therefore, the majority of negative winter and spring net energy retention values are, in the context of the errors involved, close

to zero energy balance. Therefore, both positive and negative energy retention values were included in relationships.

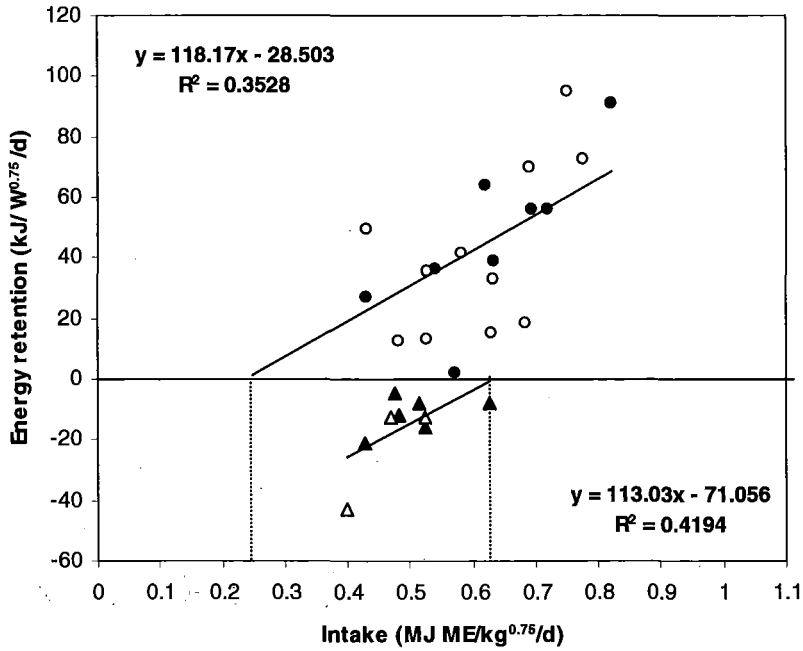


Figure 5.15a *Energy retention (kj/W $^{0.75}$/day) in whole body weight gain of red deer (solid symbols) and hybrids (open symbols) in winter across a range of ME intakes. Separate relationships are fitted for positive* (O) *and negative* (▲) *energy retention values.*

When a common relationship was fitted to both positive and negative energy retention values there was no significant genotype difference between net retained energy (kJ /W $^{0.75}$/day), and intake (MJ ME/W $^{0.75}$/day) ($P > 0.05$). Deer consuming 0.48 MJ ME/W $^{0.75}$/day had zero energy retention during winter and retained 23.7 kJ net energy for every additional 100kJ of ME intake (Figure 5.13). Relationships within the individual genotypes were;

Red	Energy retention (kJ) = 245.2 (55.8) ME intake- 120.1(32.8)	n=14	R^2=57%
Hybrid	Energy retention (kJ) = 230.0 (61.9) ME intake - 105.7 (36.6)	n=14	R^2= 54%

Based on these equations ME intake for zero energy balance would have been 0.49 and 0.46 MJ ME/W $^{0.75}$/day for red and hybrid deer, respectively and energy retention would have been 24.5 and 23.0 kJ net energy for every additional 100 kJ in ME intake for red and hybrid deer, respectively.

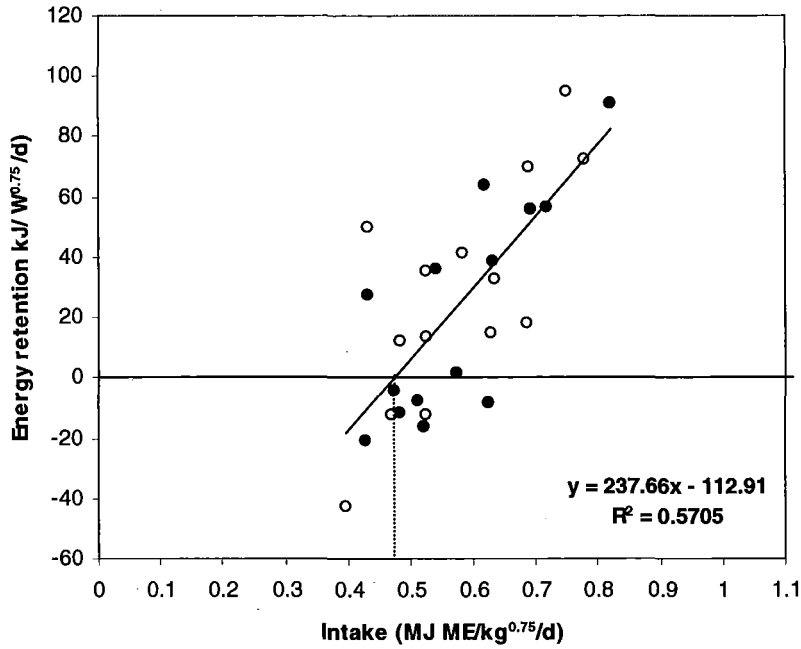


Figure 5.15b. *Relationship between net energy (kj/W $^{0.75}$/day) retained in whole body of red deer (●) and hybrids (O) offered a range of feeding levels during winter. The fitted relationship includes both positive and negative energy balance values.*

During spring, there was no difference between genotypes (P > 0.05) in the relationship between net energy retention and ME intake (Figure 5.16). Either genotype had an intake of 0.59 MJ ME/W $^{0.75}$ /day at zero energy retention and retained 36.9 kJ for every additional 100 kJ in MEI

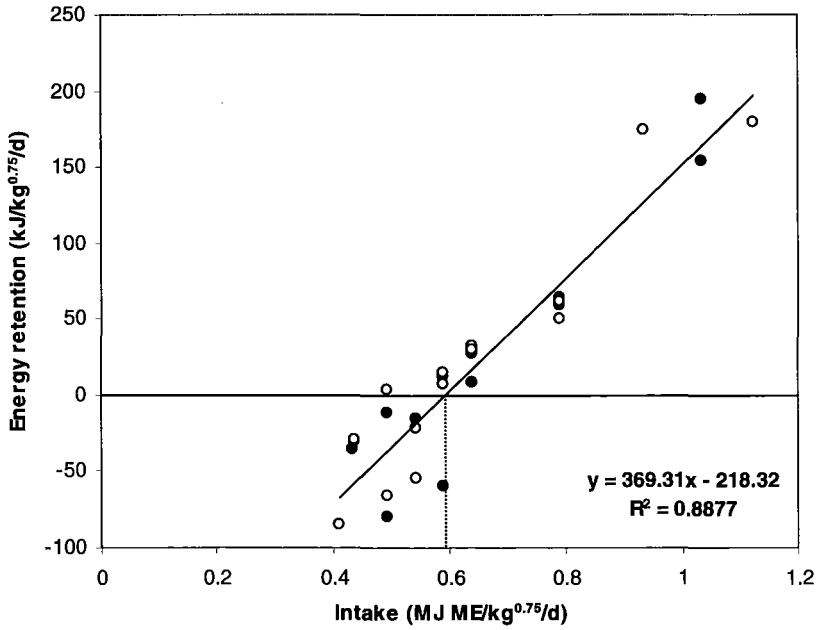


Figure 5.16 *Relationship between net energy (kj/W $^{0.75}$/day) retained in whole body during spring of red deer (●) and hybrids (O) over a range of ME intake. The fitted relationship includes both positive and negative energy balance values.*

Relationships for the individual genotype were;

Red Energy retention (kJ) = 369.3 (38.3) ME intake – 220 (25.9) n=14 R^2 = 89%

Hybrid Energy retention (kJ) = 369.5 (37.4) ME intake – 217 (25.2) n=14 R^2 = 89%

Based on these equations ME intake for zero energy balance would have been 0.60 and 0.59 MJ ME/W $^{0.75}$/day for red and hybrid deer, respectively and energy retention would have been 37.0 kJ net energy for every additional 100 kJ in ME intake.

Energy retention – effect of season

There was an apparent seasonal difference in ME_m and k_g (Figure 5.17). The relationships for winter and spring were;

Winter Energy retention (kJ) = 237.7 (40.4) ME intake – 112.9 (23.8) n = 28 R^2= 57%

Spring Energy retention (kJ) = 369.3 (25.8) ME intake – 218.3 (17.4) n = 28 R^2= 89%

Energy requirement for zero energy balance was higher ($P < 0.05$) in spring (0.59 MJ ME/W $^{0.75}$/day) compared with winter (0.48 MJ ME/W $^{0.75}$/day). The efficiency of utilisation of ME for energy gain was different between winter and spring ($P < 0.05$). The estimate of k_g was 0.24 during winter and 0.37 in spring

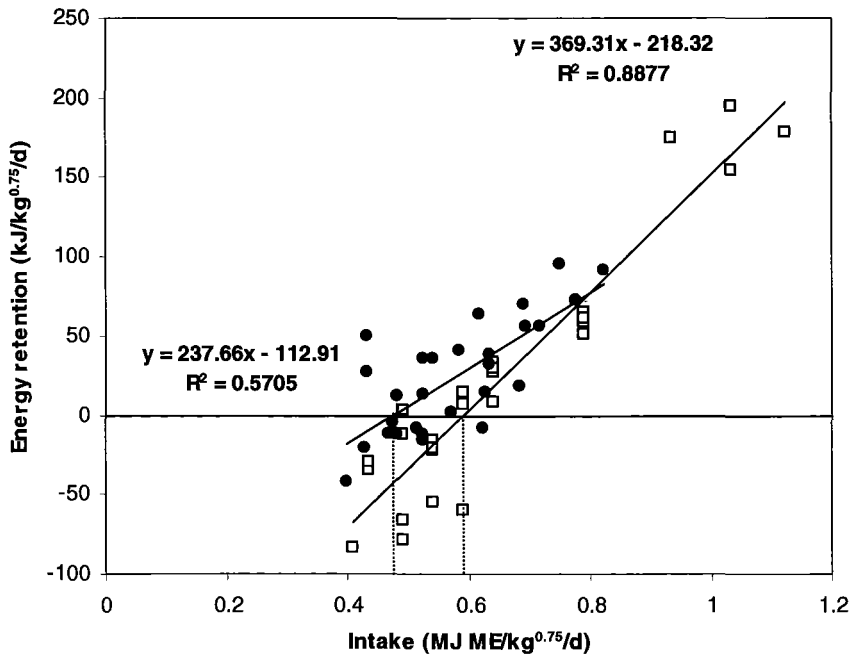


Figure 5.17 *Relationship between ME intake and net energy retained in whole body during winter (●) and spring (■) for all deer. The fitted relationship includes both positive and negative energy balance values.*

Utilisation of energy for fat and protein deposition

The energy cost of fat and protein deposition in deer was calculated from the composition of gain and ME intake. Multiple regression analysis was used to partition ME intake (less a common ME_m of 0.48 and 0.59 MJME/$W^{0.75}$/day during winter and spring, respectively) between fat and protein retention separately for deer in positive energy balance in winter and spring. Preliminary analysis indicated there was no significant difference between genotypes and therefore genotypes were combined for analysis. Intake was partitioned as;

$$(\text{ME intake} - ME_m) = b1\ F + b2\ P$$

where ME intake was the daily intake expressed on a metabolic whole body weight basis (kJ/$W^{0.75}$/day), ME_m was maintenance requirement from the energy retention relationship as described above, F was the daily amount of energy deposited as fat (kJ/$W^{0.75}$/day), P was the amount of energy deposited as protein daily (kJ/$W^{0.75}$/day) and b1 and b2 were the regression coefficients. The weight used in calculating metabolic body weight ($W^{0.75}$) was the combined weight of adipose, lean and bone tissue estimated from whole body CT images which included estimated GIT weight. The coefficient b1 and b2 were interpreted as the energy cost of depositing 1kJ of fat and protein, respectively and the reciprocal an estimate of k_f and k_p.

The multiple regression coefficients for winter and spring are shown in Table 5.9.

Table 5.9. *The regression coefficients for the multiple regression of fat and protein deposition on ME intake for deer during winter and spring in positive energy balance.*

Season	*n*	Fat	Protein	R^2
Winter	19	$9.7 \pm 1.9^{***}$	-1.9 ± 1.5	87%
Spring	16	$1.57 \pm 0.71^{*}$	$4.07 \pm 0.75^{***}$	96%

where *, $P < 0.05$ and ***, $P < 0.001$.

During winter, partial efficiency was only significantly different from zero for fat deposition. Protein deposition did not explain a significant proportion of the variation in ME intake. Removing those animals that had a positive energy balance despite losing fat from the analysis did not improve the equation significantly. Both coefficients were significantly different to zero during spring, with 95 - 96% of the variation in ME intake explained in energy deposited in fat and protein. The inability to apportion any variation in ME intake to protein deposition (coefficient non-significant) during winter resulted in a poor winter-spring combined regression. Where both coefficients were significant (spring) the estimates of energy cost of fat and protein deposition (± SEM) were 1.57 ± 0.71 and 4.07 ± 0.75 MJ MEI/MJ for fat and protein, respectively. Therefore the partial efficiencies of utilisation of ME for energy deposition as fat and protein were 0.64 and 0.26, respectively.

Energy value of gain

There was a positive relationship between the net energy retained (MJ) and whole body weight gained (kg) during winter (Figure 5.18) and spring (Figure 5.19). There was no significant difference between genotypes.

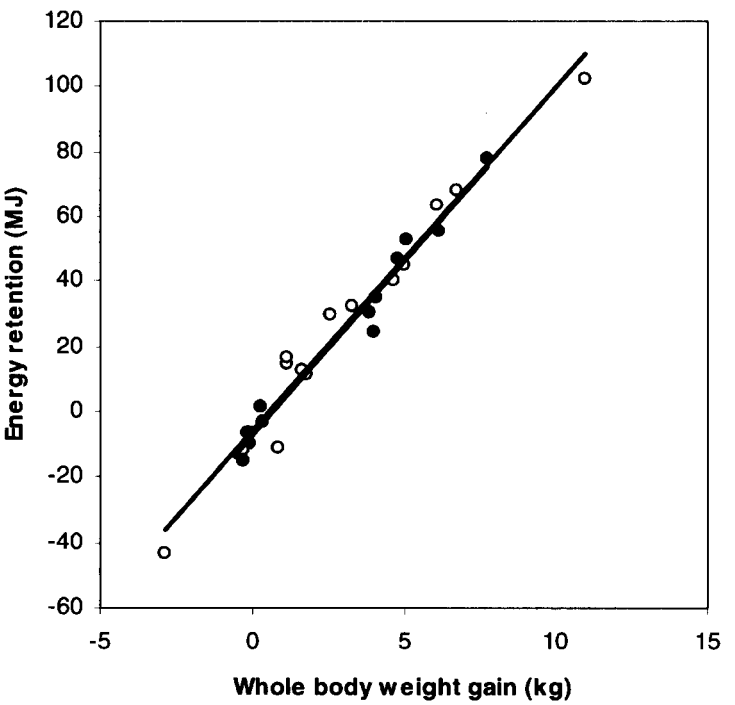


Figure 5.18. *Relationship between whole body weight gained (kg) and energy retained (MJ) during winter (49 days) for red deer (●) and hybrid deer (O).*

For winter the individual relationships were;

Red deer	Energy retention = 10.7 (0.5) WBG - 8.0 (1.7)	n = 14	R^2 = 98%
Hybrid	Energy retention = 10.5 (0.5) WBG -6.02 (2.7)	n = 14	R^2 = 96%

There was no significant genotype difference and whole body weight gain in winter contained 10.6 MJ/kg for either red or hybrid deer.

For spring, the individual relationships were;

Red deer	Energy retention = 9.9 (0.5) WBG + 7.5 (3.5)	n = 14	R^2 = 97%
Hybrid	Energy retention = 8.8 (0.5) WBG + 5.9 (4.2)	n = 14	R^2 = 96%

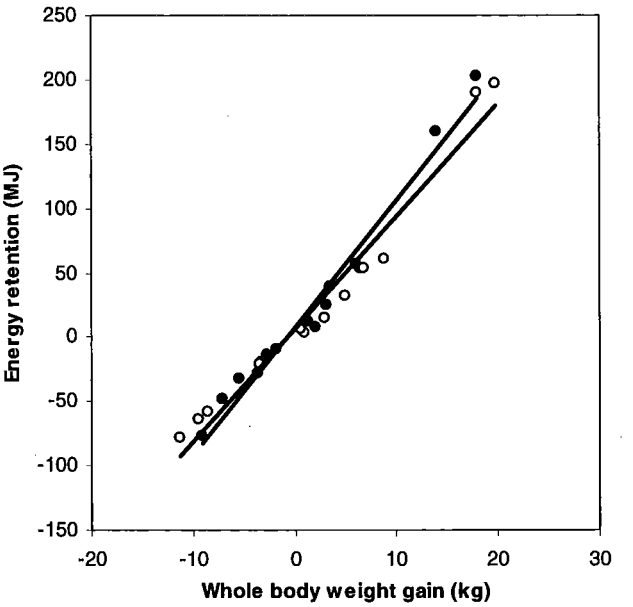


Figure 5.19. *Relationship between whole body weight gained (kg) and energy retained (MJ) during spring (49 days) for red deer (●) and hybrid deer (O).*

There was no significant genotype difference and whole body weight gain in spring contained 9.4 MJ/kg for either red or hybrid deer.

Data from each genotype was combined to establish the seasonal effect (Figure 5.20)

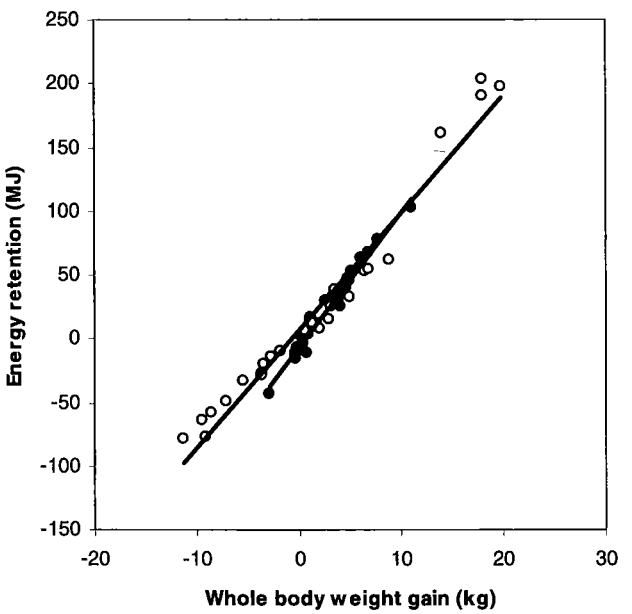


Figure 5.20. *Relationship between whole body weight gained (kg) and energy retained (MJ) during winter (●) and spring (O).*

The individual relationships were;

Winter	Energy retention = 10.6 (0.4) WBG - 7.1 (1.5)	n = 14	R^2 = 97%
Spring	Energy retention = 9.2 (0.3) WBG + 6.7 (2.8)	n = 14	R^2 = 97%

There was significant seasonal difference and whole body weight gain was 9.2 MJ/kg and 10.6 MJ/kg for the winter and spring, respectively.

5.3 Discussion

Ad lib. feed intake

Ad lib. feed intake in this experiment was lower in winter but higher in spring compared with those reported in Chapter 4 (Table 5.10). Consequently, the increase in voluntary feed intake (MJ ME/kg /day) from winter to spring for red deer (44%) and for hybrids (55%) was higher than that recorded in Chapter 4 (22 and 23 % for red and hybrid deer, respectively) and higher than the 30% recorded by Domingue *et al.* (1991a) and Freudenberger *et al.* (1994) for red deer. It is unclear as to the reason for the variation in *ad lib.* intake between the two experiments although similar variation between years has been reported previously for deer (Webster *et al.*, 1997).

These data confirm previous reports of a seasonal cycle of *ad lib.* intake which increases from winter to spring for deer, but also indicate the amplitude of liveweight change is relatively larger for hybrid than for red deer.

Liveweight gain at ad lib. feeding

This experiment provided further evidence that red deer may have a faster relative rate of liveweight gain than hybrid deer in winter when feed was offered *ad lib.* (Table 5.10). The mean relative liveweight gain of hybrid deer fed *ad lib.* in this experiment was lower than expected based on hybrid deer at lower feeding levels. This was despite hybrids being in good health and having a similar intake to red deer. It is difficult therefore, to interpret this observation in isolation but it does support the trend reported in Chapter 4.

Although red deer may gain liveweight relatively faster than hybrids in winter, because of the differences in liveweight (approximately 10 kg), absolute liveweight gain was similar between genotypes.

Table 5.10 *Comparison of voluntary feed intake and liveweight gain of red and hybrid deer in this experiment and in the experiment detailed in Chapter 4.*

	Chapter 4		**Chapter 5**	
	Intake (g DM/W $^{0.75}$ /day)	Liveweight gain (g/W $^{0.75}$ /day)	Intake (g DM/W $^{0.75}$ day)	Liveweight gain (g/W $^{0.75}$ /day)
		Winter		
Red	79.1	7.99	61.6	8.61
Hybrid	76.7	7.02	62.5	5.64
		Spring		
Red	95.7	10.70	88.5	12.43
Hybrid	94.5	12.33	96.3	15.23

As in previous experiments, hybrids fed *ad lib.* grew faster during spring on both an absolute and metabolic liveweight weight basis compared with red deer. The difference was larger in this

experiment (2.8 g/W $^{0.75}$ /day) compared with that in Chapter 4 (1.6 g/W $^{0.75}$ /day). This might have been expected considering *ad lib.* intake in this experiment was greater for hybrids (96.3 g DM /W $^{0.75}$ /day) than for red deer (88.5 g DM /W $^{0.75}$ /day) when in Chapter 4 it had been similar.

This experiment provided further evidence that hybrids exhibit a greater amplitude in seasonal cycle of relative and absolute liveweight gain.

Restricted feeding

When intake was restricted during winter, liveweight gain decreased by 2.28 and 1.84 g/W $^{0.75}$ /day for every 0.1 MJ ME/W $^{0.75}$ /day reduction in intake for red and hybrid deer, respectively (Figure 5.3). Effectively, the energy cost of liveweight gain tended to be lower for red deer (44 MJ/kg of liveweight) compared with hybrid deer (55 MJ/kg of liveweight) in winter but the difference was not significant. The estimated ME requirement for maintenance of liveweight during winter was similar for both genotypes (0.38 - 0.40 MJ ME/W $^{0.75}$ /day) suggesting if red deer gained liveweight faster than hybrids this was a result of a difference cost of liveweight gain rather than maintenance requirement. The possibility that red deer are able to grow more quickly over winter compared with hybrids must be tempered against the fact that winter is a period where the potential for liveweight gain is low and in the field liveweight gain below 100 g/day is common. It should also be recognised that winter in this experiment refers to the period of June -July. Hybrids may appear to gain liveweight faster than red deer in "winter" if late autumn and early spring months are also included, where hybrids would be expected to have a greater liveweight gain than red deer.

The estimates of the energy required for maintenance and liveweight gain, the efficiency of utilisation of energy for maintenance and liveweight gain and the energy value of the gain from this experiment have been summarised in Table 5.11.

Table 5.11. *A summary of the energy requirement for maintenance (energy balance and liveweight balance), costs of liveweight gain and energy value of whole body gain.*

		Red deer	Common*	Hybrid deer
Winter	ME for zero LWG (MJ ME/W $^{0.75}$/day)	0.37	0.38	0.39
	Cost of LWG	44	49	55
	ME for zero WBWG (MJ ME/W $^{0.75}$/day)	0.41	0.42	0.43
	Cost of WBWG	51.7	50.9	50.2
	ME for zero energy gain ((MJ ME/W $^{0.75}$/day)	0.49	0.48	0.46
	k_g	0.25	0.24	0.23
	Energy value of WBWG	10.7	10.6	10.5
	Energy value of LWG	6.6		6.2
Spring	ME for zero LWG (MJ ME/W $^{0.75}$/day)	0.35		0.47
	Cost of LWG	64		35
	ME for zero WBWG (MJ ME/W $^{0.75}$/day)	0.62	0.61	0.60
	Cost of WBWG	27.9	26.7	25.5
	ME for zero energy gain ((MJ ME/W $^{0.75}$/day)	0.59	0.59	0.59
	k_g	0.37	0.37	0.37
	Energy value of WBWG	9.9		8.8
	Energy value of LWG	11.1		8.4

* Where there is no common value, genotype differences are significant

ME requirement for maintenance

The estimated ME requirement for maintenance of liveweight (0.37 - 0.39 MJ ME/W $^{0.75}$/day) and whole body weight (0.41 - 0.43 MJ ME/W $^{0.75}$/day) during winter for both genotypes (Table 5.11) was lower than previous estimates for penned red deer in winter (0.57 MJ ME/W $^{0.75}$/day, Fennessy *et al.*, 1981; 0.63 MJ ME/W $^{0.75}$/day Semiadi *et al.*, 1994) and penned wapiti (0.56 MJ ME/W $^{0.75}$/day Jiang and Hudson, 1994; 0.57 MJ ME/W $^{0.75}$/day Jiang and Hudson, 1992) but more similar to the values recorded for red deer by Simpson *et al.*, 1978b (0.4 - 0.5 MJ ME/W $^{0.75}$/day) and Cool and Hudson, 1996 (0.47 - 0.51 MJ ME/W $^{0.75}$/day).

It is unclear why requirement for maintenance is lower than that previously reported for penned red deer. One possible explanation is the under-estimation of ME intake. Although DM intake was measured accurately, estimates for ME intake may be less accurate. Estimates of ME intake are based on the M/D value estimated from proximal analysis of feed which do not always provide reliable estimates for compound feeds (Isherwood pers com). However, the M/D values used for all experiments are what would be expected based on the feed table values of the diet constituents and their relative proportions. Further, M/D values would have had to have been grossly underestimated in order to fully explain the differences in ME intake between this and other studies. For example, deer in winter required 32.4 g DM/W $^{0.75}$/day for liveweight maintenance. Based on the estimated ME/DE of 11.7 MJ ME/kg DM, this equated to a maintenance requirement of 0.38 MJ ME/W $^{0.75}$/day. If the actual liveweight maintenance had been 0.5 MJ ME/W $^{0.75}$/day, based on the same DM intake M/D would have to have been 15.4 MJ ME/kg DM which is much higher than would be expected for a grain-based ration.

Spring ME requirement for maintenance of liveweight was 0.35 and 0.47 MJ ME/W $^{0.75}$/day for red and hybrid deer, respectively. This experiment confirms the findings of Chapter 4 that during spring, red deer require less energy than hybrids for maintenance of liveweight. The difference in maintenance requirements between genotypes seen here (0.12 MJ ME/W $^{0.75}$/day) is similar to that reported in Chapter 4 (0.2 MJ ME/W $^{0.75}$/day).
Semiadi *et al.* (1994) showed differences in maintenance requirement between deer species. Young sambar deer (*Cervus unicolor*) had a lower requirement for maintenance (0.47 MJ ME/W $^{0.75}$/day) compared with red deer (0.57 MJ ME/W $^{0.75}$/day). As a consequence, at any particular rate of intake sambar retained more energy than red deer.

Webster (1981) has suggested that GIT and liver combine to contribute about 40 % of total heat production in sheep and this therefore makes fasting metabolic rate sensitive to changes in weight of these organs. Although the weight of GIT increased as whole body weight increased (25 % between lowest and highest intake) there was no genotype difference (see Figure 5.2). There is no evidence from these results that gut tissue mass contributed to any difference in ME_m between genotypes.

When the amount of net energy retained in whole body or whole body weight gain was considered as a response to intake rather than liveweight gain there was no significant genotypes effect. Consequently, either genotype required 0.48 MJ ME/W $^{0.75}$/day in winter and 0.59 MJ ME/W $^{0.75}$/day in spring in order to achieve zero energy balance or 0.42 MJ ME/W $^{0.75}$/day in winter and 0.61 MJ ME/W $^{0.75}$/day in spring in order to achieve zero whole body weight change. These are similar to other estimates (Simpson *et al.* 1978b). There was no clear genotype trend in ME for either zero energy gain or zero whole body weight gain.

ME requirement for gain

Estimates of the energy costs of liveweight gain were similar to those previously published (Table 2.2) ranging from 35- 64 MJ ME/kg. The energy cost of liveweight gain during winter was not significantly different between genotypes but there was a trend for red deer to have a lower cost than hybrids. This is consistent with the observation that red deer tended to grow faster than hybrids during winter at *ad lib.* intake. Because maintenance requirements were similar between genotypes, it would be expected on restricted intake, that liveweight gain differences would be even smaller. The energy cost of whole body gain during winter (50.9 MJ ME/kg) was not significantly different between genotypes and was similar to the energy cost of liveweight gain (49.0 MJ ME/kg).

A similar maintenance requirement, but lower cost of liveweight gain suggests red deer may grow faster than hybrids if fed *ad lib.* over winter. However, in a commercial situation high winter feeding levels are likely to be financially unacceptable and therefore on restricted diets it would be expected that genotypes would gain liveweight at a similar rate over winter. It would also be dangerous to extrapolate these data to comparisons of hybrid deer which contain a higher proportion of elk genes. While the hypothesis that elk type deer have a higher energy cost of gain during winter compared with red deer may be a valid one, there is some evidence that the seasonal cycle in intake is not so pronounced in these elk type deer compared with red deer (Beatson *et al.,* 2000) and winter liveweight gain may be more rapid as a consequence.

During spring, when a linear relationship was fitted to ME intake-liveweight gain relationships, liveweight gain changed by 2.0 and 4.3 g/W$^{0.75}$/day for every 0.1MJ ME/W$^{0.75}$/day decrease in intake for red deer and hybrids, respectively. The value for red deer is of a similar magnitude to that calculated from the data of Webster *et al.*, (1997) of 1.8 and 2.2 g/W$^{0.75}$/day for every 0.1 MJ ME/W$^{0.75}$/day in two different years. Wapiti calves (4 months) reduced average liveweight gain by 3.5 g/W$^{0.75}$/day for every 0.1 MJ ME/W$^{0.75}$/day restriction in intake (Cool and Hudson, 1996). This result suggests the efficiency of utilising metabolisable energy for spring liveweight gain is lower for red deer compared with hybrids. Therefore, in spring and on a high intake hybrids would be expected to gain liveweight faster than red deer due to their lower cost of gain. When feeding is restricted, however, the greater energy requirement for maintenance of hybrids reduces the difference in liveweight gain compared with red deer.

The implication to producers is that the greatest advantage in liveweight gain (per head) to hybrids relative to red deer occurs in spring and when hybrids approach *ad lib.* intake. Underfed hybrids will gain less liveweight than equally underfed red deer.

The energy cost of whole body weight gain in spring (26.7 MJ ME/kg) was not significantly different between genotypes and was lower than the cost of liveweight gain (35 – 64 MJ ME/kg). This was

not consistent with the genotype differences in spring liveweight gain. Genotypes did not differ in their energy requirement for energy gain but this is not surprising since whole body weight gain and energy gain are derived from the same measurements of body composition. Changes in gut fill over spring as outlined in Chapter 5a are a possible source of this effect. Gut and its contents appeared to increase during the spring period (Table 5.4) and more so for the lower feeding treatments than for the *ad lib.* treatment. This would have the effect of increasing the cost of liveweight gain relative to whole body weight gain which is consistent with the results of this experiment. Further, as intake increased, the size of the increases in gut contents was greater for red deer than for hybrids which are consistent with the liveweight gain results from this experiment.

Composition of gain

The energy cost of gain depends upon the composition of gain or (the energy value of gain) and the efficiency by which energy is deposited as fat (k_f) and protein (k_p). Gain with a high proportion of fat is associated with a high cost while gain high in protein is associated with a lower cost.

There was no significant difference between red and hybrid deer in the composition of whole body gain (Figure 5.10), but in winter there was a trend for red deer to deposit less fat than hybrids and in spring for hybrid deer to deposit less fat than red deer. However, there was no significant difference and no clear trend in net energy retention. Essentially k_g was not different between genotypes.

The efficiency by which energy is deposited as fat and protein also affects the energy cost of gain. When energy intake (after subtracting a common ME_m) was partitioned between fat and protein deposition for spring both the fat and protein deposition coefficient were significant and gave mean partial efficiency of 0.64 and 0.26 for fat and protein, respectively. There estimates were similar to some previously published for lambs, calves and pigs (Table 2.3).

These was no significant difference between genotypes in the efficiency by which metabolisable energy was used for fat or protein deposition but this observation was based on a small sample size. Previous estimates of the partial efficiency of fat and protein deposition (Table 2.3) have shown significant variation, especially for protein deposition. However, this variation is associated with comparisons of pre- and post - ruminant animals and animals fed milk and roughage diets. It is unlikely that deer at a similar stage of development on the same diet differ in the partial efficiency of fat and protein deposition. In this experiment there is no evidence to suggest genotype differences in k_p or k_f and therefore differences in the composition of gain should be reflected by different k_g values.

5.4 Summary

Based on the work in this chapter red yearling stags relative to hybrid stags have a similar energy requirement for maintenance and gain of liveweight, whole body weight and energy in winter. Therefore observed differences between genotypes in liveweight gain in winter are likely to reflect differences in intake.

In spring, the ME requirement for maintenance of liveweight was higher for hybrids than red deer but the requirement of maintenance of whole body weight or energy was similar. Similarly, the cost of liveweight gain was greater for red deer than for hybrids but there was no genotype difference in the costs of whole body weight gain and energy retention. The difference in results between liveweight and whole body weight or energy retention is possibly explained by changes in gut fill during the experiment. Therefore, observed differences in liveweight gain between genotypes in spring are likely to reflect either differences in intake or differences in gut fill. The effects of feeding level and genotype on gut fill needs to be further investigated.

Although season did not have an effect on either the energy required to maintain liveweight or the cost of liveweight gain, both whole body weight gain and energy retention was more costly but required less energy for balance in winter than in spring.

Chapter 6

The effect of season and intake on the apparent *in vivo* digestibility of a pelleted feed offered to deer

6.0 Introduction

Previous studies have shown seasonal variation in digestibility of DM intake for sheep (Milne *et al.*, 1978), goats (Domingue *et al.*, 1991a), and deer (Domingue *et al.*, 1991a; Freudenberger *et al.*, 1994). Between-genotype difference in the seasonality of digestibility of feed is a possible mechanism by which red and hybrid deer may differ in their liveweight response to intake in winter and spring. The aim of this experiment was to determine the genotype and seasonal effect on apparent DM digestibility. This chapter reports two independent studies of feed digestibility for red and hybrid deer in winter and spring.

6.1 Materials and Methods

Apparent *in vivo* OM and DM digestibility was measured during winter and spring for two separate groups of deer in consecutive years. Group 1 was a subset (n= 20) of deer involved in the experiment described in Chapter 5. Within genotype, deer were paired on liveweight and offered one of a range of intakes between 0.4 times *ad lib.* to *ad lib.* feeding. Group 2 comprised individually penned deer (n = 10) as described in Chapter 4 which were offered one of a range of feeding levels between 0.5 to 0.9 times *ad lib.* Deer in both groups were fed a pelleted diet. A more detailed description of feeding and housing is provided in the respective chapters.

Group 1

In Group 1, four deer per week (all animals on one feeding level) were housed in individual pens which had been cleared of sawdust and fitted with a false floor of wire mesh. Total daily faecal output was collected by gathering any faecal material aggregated on the wire mesh and combining it with all faecal material on the pen floor. Where deer moulted, care was taken to exclude pelage in faecal collections. During the faecal collection process, deer were placed separately in concrete-floored holding pens and any faeces produced was collected and added to the collection for that day. Faecal collections were made daily prior to feeding for 7 days. Total daily faeces for each animal was dried at 70°C for 48 h and weighed. After weighing, a 50 g sub-sample from each day's collection was bulked for each animal and stored in an air-tight container for organic matter analysis.

Dry matter intake was determined by subtracting any feed refused from the daily fresh feed offered and correcting for average dry matter (87%). There was no difference in dry matter between fresh and refused feed.

Apparent dry matter (DM) digestibility was calculated as follows;

$$\text{apparent DM digestibility} = \frac{\text{total DM intake - total faecal DM}}{\text{total DM intake}}$$

A 2 g sample of the bulked sub-samples of dried faeces for each animal along with ground samples of feed (2 g) were placed in porcelain crucibles and oven dried for 24 h at 90°C. Samples were removed and allowed to cool in a desiccator before being weighed (nearest 0.1 mg). Samples were reduced to ash at 550°C for 8 h and were allowed to cool before being re-weighed. Organic matter (OM) digestibility was calculated as;

$$\text{apparent OM digestibility} = \frac{\text{total OM intake - total faecal OM}}{\text{total OM intake}}$$

Group 2

Each day for 10 days deer from Group 2 (5 of each genotype) with known DM intake received, 140 ± 1.0 mg of *n*-alkane (dotricontane, C_{32}) mixed with approximately 3 g of ground feed administered in a 5 g gelatine capsule. Faecal samples (> 10 g fresh weight, collected from the rectum by grab sampling) were taken daily for 5 days following an initial 5 days of dosing.
Samples were frozen at -20°C whilst awaiting analysis.

Apparent DM digestibility was calculated from faecal output and DM intake as follows.

$$\text{apparent DM digestibility} = \frac{\text{DM intake (kg) – faecal output (kg DM)}}{\text{DM intake (kg)}}$$

Faecal output was calculated from alkane dose (C_{32}) and faecal alkane (C_{32}) concentration having accounted for a 15% apparent loss of alkane within the GIT (Mayers *et al.*, 1986);

$$\text{Faecal output (kg DM)} = \frac{C_{32}\text{ dose (mg/day) - (}C_{32}\text{ dose (mg/day) x 0.15 (endogenous alkane loss)}}{\text{faecal } C_{32} \text{ extraction (mg/kg DM)}}$$

Sample analysis

Each individual faecal sample was freeze dried and ground (< 1 mm). Samples were bulked so that for each deer the bulked sample contained equal proportions of faeces from the 5 collection days. Approximately 2 g from each bulked sample was weighed into a crucible and oven dried for 24 h to determine percentage dry matter. Both a 1 g sample of bulked faeces and 0.4 ml of an *n*-alkane standard were weighed accurately (± 0.1 mg) into a 70 ml Kymax tube. The alkane standard

contained 0.1026 g of C_{24} (*n*-tetracosane) and 0.1041 g of C_{34} (*n*-tetratriacontane) dissolved in 80.14 g of C_{11} (*n*-undecane) (Sigma Chemical Company Ltd). The sample and standard was left for 12 h at room temperature in 10 ml of a 1.5 M solution of KOH in methanol (analytical reagent grade, BDH New Zealand Ltd). Tops of the tubes were tightly sealed and the tubes placed in an oven at 90°C for 3.5 h. The mixtures were shaken hourly and any methanol loss replaced. The tubes were subsequently removed and placed in a water bath at 60°C.

To each tube 5 ml analytical grade *n*-heptane (Riedel-de Haën, Germany) and 5 ml nano-pure water were added, the tube shaken vigorously and returned to the water bath to allow a bi-phase to form. The top layer of the bi-phase was removed using a vacuum manifold and purified through a silica gel (3.5 g Kiesegel 70-325 mesh packed in a 25 ml syringe fitted with a sintered glass frit at the bottom). Another 5 ml of *n*-heptane was added to the mixture, shaken and replaced in the water bath. The bi-phase was removed and purified as before. The column was then rinsed with 10 ml of *n*-heptane to elute any remaining alkanes. The elute was placed in an oven at 90°C for 36h to evaporate the *n*-heptane. When all *n*-heptane had been evaporated a further 0.7 ml of *n*-heptane was added to each cooled tube, the tube walls washed and sample transferred to GLC autosampler vials using a Pasteur pipette. Samples were analysed on a Hewlett Packard HP 6890 GC system.

The GC was set to inject a 1µl sample into the front inlet at 300°C and in splitless mode. The column used was a BP1 megabore capillary column 30 m in length with an internal diameter of 530 µm and silica film thickness of 1µm. Helium flow through the column was set at a constant 4.2 ml/min. The front flame ionisation detector was set at 300°C.

Statistical analysis

Relationships between intake and *in vivo* digestibility were fitted using linear regression. Differences in regression coefficients and intercept values between relationships for each season were examined using the method of Snedecor and Cochran (1980).

6.2 Results

Conclusions reached from this experiment were no different regardless of whether apparent OM or DM digestibility was used and for this thesis only DM values have been presented.

Apparent DMD was higher in winter than spring for both Group 1 (Figure 6.1) and Group 2 (Figure 6.2) with the between-season difference being about 7 percentage units within Group 1 and 4.5 - 11 percentage units within Group 2 on similar intake. The decrease in digestibility from winter to spring was independent of intake for Group 1. There was no significant difference between genotypes in this seasonal effect on digestibility.

There was positive effect of intake on digestibility in both groups ($P < 0.01$). Digestibility increased by 0.027 digestibility units for every 10 g DM/$W^{.75}$/day increase in intake for both genotypes in either season in Group 1 and 0.041 and 0.021 digestibility units for deer in winter and spring, respectively in Group 2.

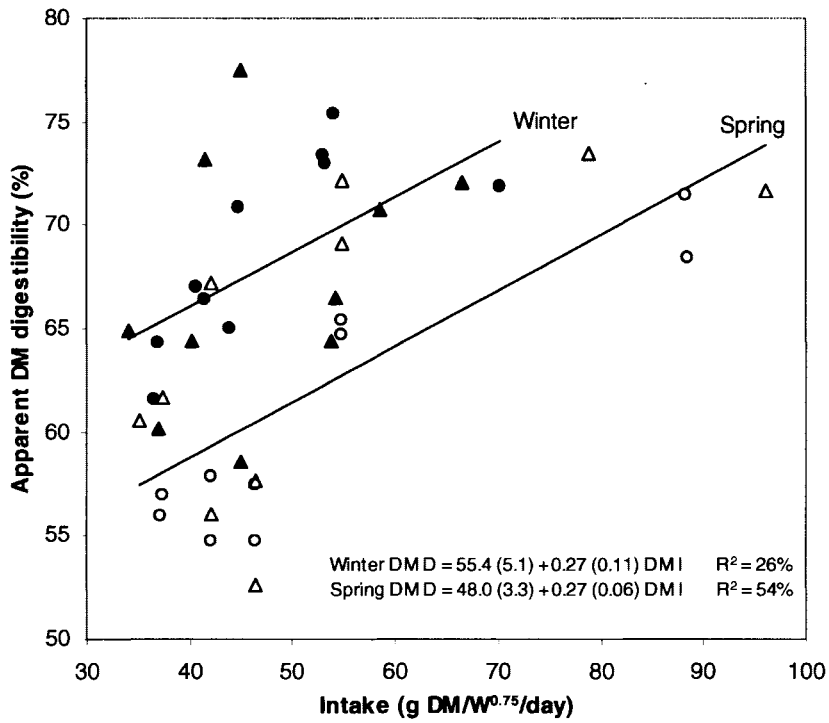


Figure 6.1. *Apparent in vivo DM digestibility of a pelleted feed offered to red (O) and hybrid (▲) deer (Group 1) on a range of intake levels during winter (solid symbols) and spring (open symbols).*

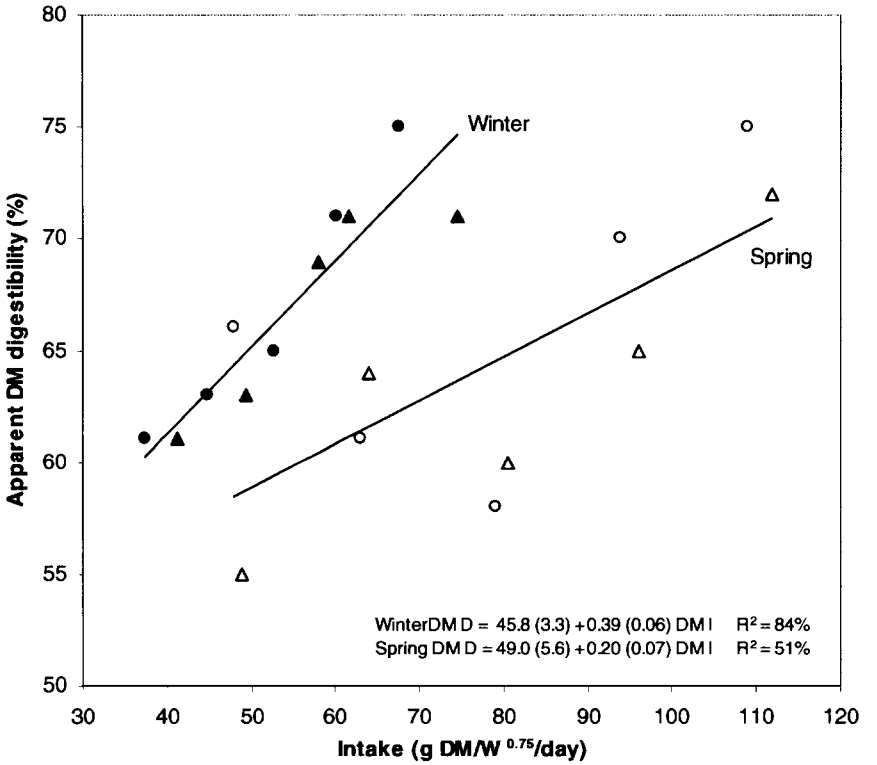


Figure 6.2. *Apparent in vivo DM digestibility of a pelleted ration offered to red (O) and hybrid (▲) deer based on faecal marker (n- alkane) concentration at 5 intake levels during winter (solid symbols) and spring (open symbols).*

When data from both groups were combined, the linear regression equations were;

$$\text{Winter DMD} = 54.25\ (3.6) + 0.269\ (0.07)\ \text{DMI} \qquad R^2 = 34\%$$

$$\text{Spring DMD} = 51.04\ (2.6) + 0.195\ (0.04)\ \text{DMI} \qquad R^2 = 50\%$$

where DMD is dry matter digestibility, DMI is dry matter intake and figures in parentheses are standard errors of the mean.

6.3 Discussion

Seasonal effect on digestibility

As with previous reports (Barry *et al.*, 1991; Domingue *et al.*, 1991a; Freudenberger *et al.*, 1994), this study found a marked increase in *ad lib.* intake of deer between winter and spring/summer. The increase in *ad lib.* intake between winter and spring recorded in this experiment (26%) (Table 6.1) was of a similar magnitude to previously reported estimates of 54% (Milne *et al.*, 1978) and 33 % (Freudenberger *et al.*, 1994) In previous experiments (Domingue *et al.*, 1991a , 1991b; Freudenberger *et al.*, 1994), it was found that, despite these marked seasonal changes in *ad lib* intake, there was no change in apparent digestibility. The result of the present study agrees with those findings (Figures 6.1 and 6.2).

Table 6.1 *Ad lib. intake in winter and spring for stags and the corresponding mean apparent digestibility of dry matter.*

		Ad lib. intake (g DM/W $^{0.75}$/day)	Average DMD at *ad lib.* intake (%)
Group 1	winter	62.1	72.0
	spring	87.9	71.2
Group 2	winter	71.1	73.0
	spring	110.4	73.5

Digestibility partially depends upon mean retention time of particles in the rumen (MRT). The longer feed particles spend in the rumen the greater the potential for them to be degraded and the higher the digestibility. MRT is a function of the fractional outflow rate of particles from the rumen (FOR). Therefore, the faster the FOR, the lower the MRT and the lower the degradability and digestibility. However, if the size of the rumen dry matter pool increases then an increase in FOR can occur without a reduction in MRT and consequently digestibility.

Previous authors have argued that deer fed *ad. lib.* are able to avoid the reduction in digestibility that would normally be associated with a seasonal increase in *ad lib.* intake by a seasonal change in passage rate of digesta through the gut as measured by FOR from the rumen. Domingue *et al.*, (1991a) reported a lower FOR of both liquid and particulate matter from the rumen in winter than summer and Freudenberger *et al.*, (1994) showed FOR of either liquid or particulate matter in winter tended to be higher than the summer values. Domingue *et al.*, (1991a) hypothesised that a decrease in FOR (independent of *ad lib.* intake) was probably the mechanism through which deer were able to increase their *ad lib.* intake during summer without incurring a decrease in digestibility. Both Domingue *et al.*, (1991a) and Freudenberger *et al.*, (1994) reconciled the increased *ad lib.* intake and

decreased FOR with an increase in the digesta pool size of the rumen. A lower FOR in summer than winter was a logical explanation for the increase in total and liquid pool sizes within the rumen in summer compared with winter

The current model for changes in seasonal digestibility, based on the work by Domingue *et al.*, (1991a) and Freudenberger *et al.*, (1994), is depicted in Figure 6.3. This shows the generally accepted negative relationship between feed intake and apparent digestibility. The hypothesised decline in FOR between winter and summer, which is independent of intake, shifts the relationship to the right. Therefore, as *ad lib.* intake increases from winter to summer, digestibility remains at point A instead of decreasing to point B (Figure 6.3) as would be expected if FOR remained unchanged

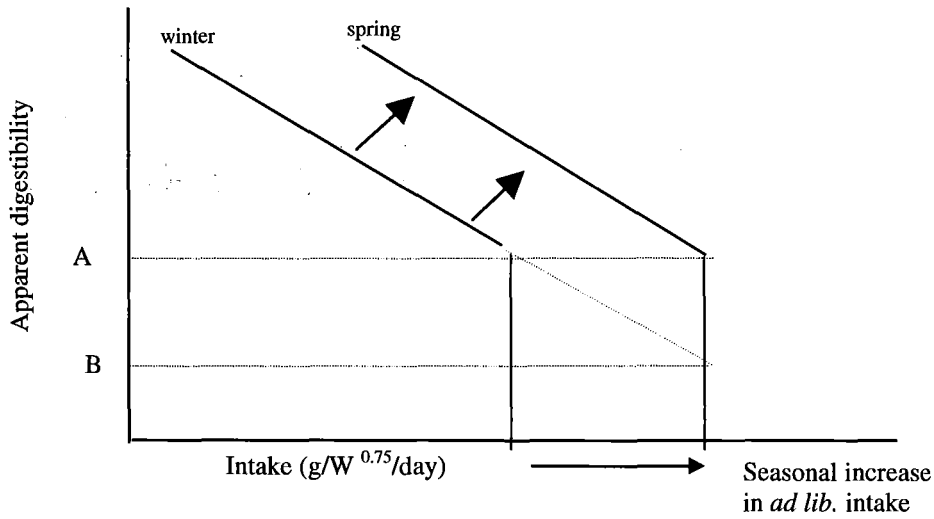


Figure 6.3 *The current model of the seasonal and level of intake effects on the digestibility of feed in deer (based on the work of Domingue et al., 1991a and Freudenberger et al., 1994)*

This model suggests that at a common intake, digestibility will be higher in spring relative to winter. In contrast, the present study showed that digestibility was lower in spring compared with winter, independent of intake. In interpreting a higher spring digestibility compared with that of winter in terms of FOR and MRT, it would seem that FOR would need to increase and MRT decrease between low winter and high spring intake to explain the lower spring digestibility. Although both Domingue *et al.* (1991a) and Freudenberger *et al.* (1994) reported FOR decreased from winter to summer, other authors have been unable to show any change in FOR (Milne *et al.*, 1978; Sibbald and Milne, 1993). A lower FOR in spring compared with winter is the opposite to what is generally expected in other species of domestic livestock (Warner, 1981). In addition, it could be argued there is little evolutionary advantage in decreasing digestibility and consequently DDM intake and ME intake during winter where the environment may already place severe restrictions on DM intake.

Although Freudenberger *et al.* (1994) measured a smaller summer FOR, some of their own observations contradict this finding. They reported that rumen pool size increased independent of intake and therefore summer rumen pool size was greater than winter rumen pool size at similar intake. This is consistent with a slower summer FOR. A rumen pool size increase was used in the above model to reconcile an increased intake and reduced FOR. However in their data, DM pool size, when expressed as a ratio of intake, remained constant between seasons and across intake levels suggesting the seasonal increase in pool size at a similar feed intake might have been partially due to a greater volume of water in the rumen rather than a decrease in the FOR of particulate matter. In addition to this, Domingue *et al.*, (1991a) reported a seasonal decrease in FOR from 3.47 %/h (winter) to 2.77% /h (summer), which translates into an increase in MRT of 8 h. However, if the decrease in FOR was real, it is surprising that apparent digestibility of both DM and OM was unchanged. Furthermore, if FOR had decreased during summer, independent of intake, a higher digestibility due to a longer retention time would be expected. In fact, when deer were restricted during summer to a feed intake equivalent to winter *ad lib.* intake, Freudenberger *et al.* (1994) found digestibility was lower rather than higher than that recorded in the winter which would suggest that FOR may have increased rather than decreased during the summer.

A major difficulty in interpreting changes in FOR is that only subtle changes are needed to have a significant influence on MRT and therefore digestibility. For example, the SED of Freudenberger *et al.*, (1994) measurements (1%/h) may have explained the majority of the difference in apparent digestibility observed.

A proposed model based on the current work is shown in Figure 6.4. This model shows a positive relationship between feed intake and apparent digestibility. Increases in intake from winter to spring have no effect on digestibility (digestibility remains at point B). This is consistent with other studies which have fed deer *ad lib.* in both winter and spring (Domingue *et al.*, 1991a); Freudenberger *et al.*, 1994). However, the model proposes that this occurs as a result of a seasonal increase in FOR (moving from the winter to spring relationship*) reducing a potentially higher* digestibility (A) rather than a seasonal reduction in FOR and *avoiding a decline* in digestibility as proposed previously. When intake is restricted in spring, this model predicts that digestibility decreases and this is consistent with results of the present and other studies (Freudenberger *et al.*, 1994).

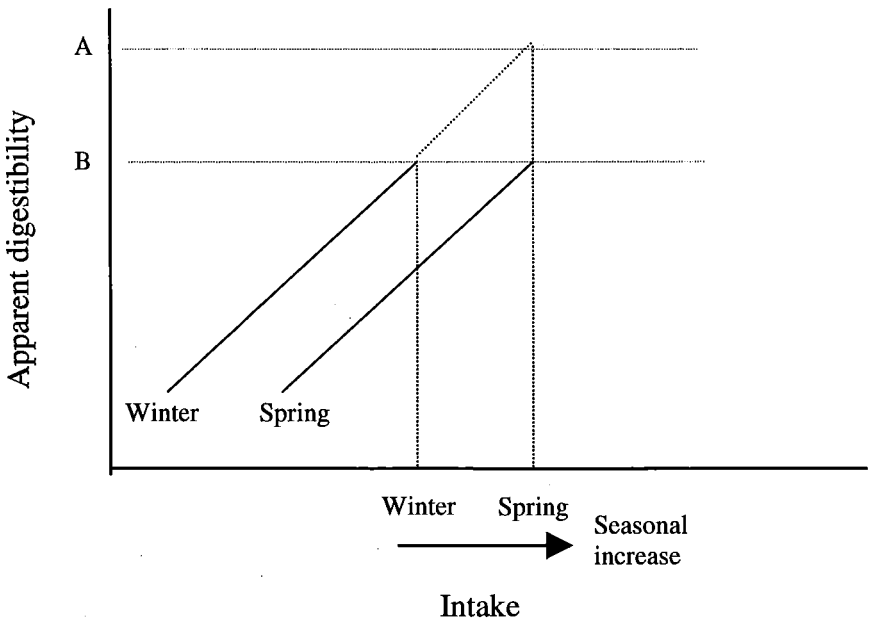


Figure 6.4 *The proposed model of the seasonal and level of intake effects on the digestibility of feed in deer based on the current work.*

Effect of level of intake on digestibility

It is generally accepted for most domestic livestock that increases in DM intake are at the expense of digestibility. The rationale for this being that the rate of passage of digesta through the gut is known to increase as the level of feed intake increases (Grovum and Williams, 1977; Warner, 1981), reducing the time for microbial digestion and resulting in a lower digestibility. Consistent with this hypothesis is the observation that mean time for which feed particles are retained in the rumen (MRT) and are exposed to microbial degradation is well correlated with digestibility of a particular feed offered to deer (Kay and Goodall, 1976). Although there is some evidence in support of an inverse relationship between intake and digestibility (for example Raymond *et al.*, 1959; Raymond *et al.*, 1955 and Faichney, 1986) there are a number of studies which provide evidence to the contrary.

For instance, digestibility decreased when feed intake was reduced in a study involving cattle (Campling *et al.*, 1963) and there was no consistent effect of reducing intake of sheep on digestibility (Blaxter *et al.*, 1956). In addition, despite a large increase in the MRT associated with reductions in intake, both sheep and cattle exhibited only a slight increase in digestibility (Campling *et al.*, 1961; Grovum and Williams, 1977). More recently Iason *et al.*, (1995) reported than in three breeds of sheep digestibility of timothy hay decreased by 4.2 percentage units as *ad lib.* intake decreased between spring and winter. Work with deer has predominantly involved *ad lib.* feeding and the effect of seasonal changes in *ad lib.* intake. The research reported here is unique in that it investigates digestibility in winter and spring over a range of DM intakes for deer. Freudenberger *et al.* (1994)

restricted deer in summer to an intake equivalent to winter *ad lib.* intake and reported digestibility of chaffed lucerne hay was lower for deer on restricted intake compared with those allowed feed *ad lib.* The data of Freudenberger *et al.* (1994) can be incorporated in the model proposed here, where digestibility decreases when intake is restricted (Figure 6.5). This supports a positive relationship between intake and digestibility but would contradict the finding that FOR was lower in spring compared with winter.

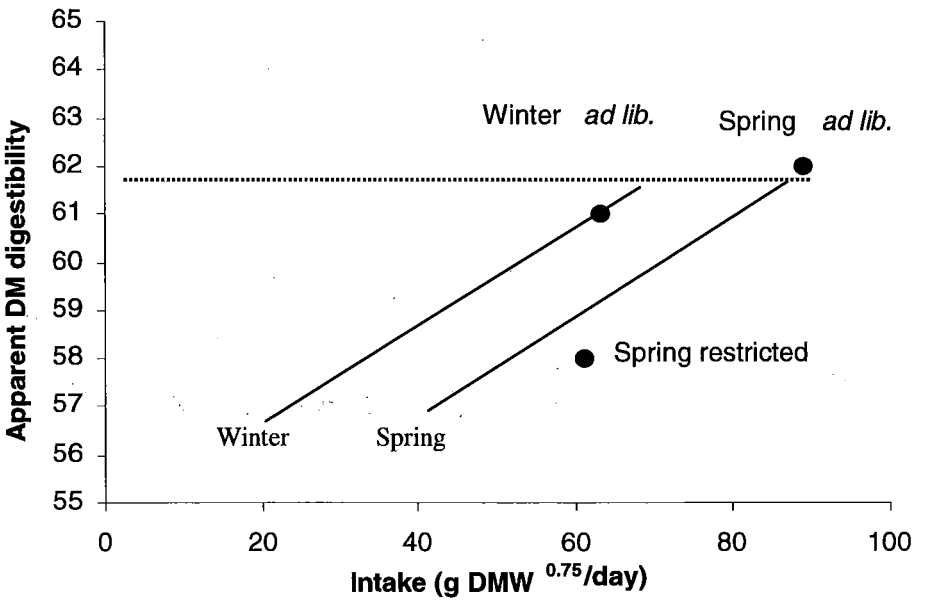


Figure 6.5 *The digestibility data of Freudenberger et al. (1994) superimposed on the proposed model of digestibility and intake.*

It is possible that the positive relationship between intake and digestibility recorded in the present study was an artefact resulting from some systematic error. Errors in digestibility experiments can result from poor measurement of faecal output or feed intake. To underestimate digestibility at low intake, faecal production would need to be overestimated or feed intake underestimated.
Inclusion of non-faecal material in the faecal DM was unlikely in this work. However, pelage (especially when deer moulted in the spring), dirt and bedding from other pens were present to some degree in all faecal collections so the sensitivity of the relationship to inclusion of such foreign material needed to be tested. This can be demonstrated in Figure 6.5 which shows that had there been no effect of intake on digestibility (regression coefficient = 0), faecal output would have to include in excess of 160 g DM/collection of non-faecal material. At the lowest feed intake, this would represent around 40% of the measured faecal output. Even more non-faecal material would have to have been included if the slope was negative as traditionally shown. While some contamination may have occurred in the present study, 10 g DM/collection is a conservative estimate, and this would have had little impact on the final relationship (see Figure 6.6).

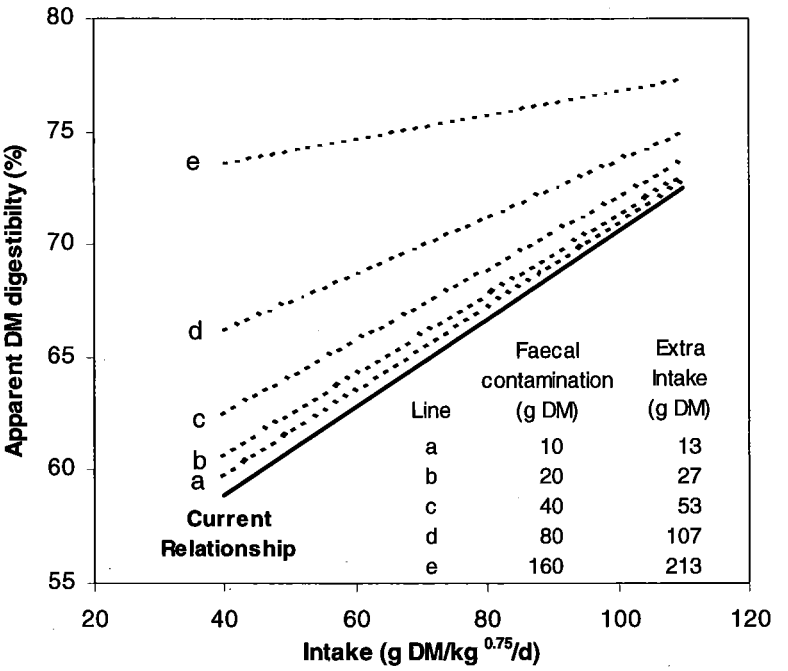


Figure 6.6. *The effect on the relationship between apparent DM digestibility and intake (combined group spring data) of including various absolute amounts of non- faecal material in faecal collections or consumption of non-feed dry matter. Extra consumption assumed an apparent digestibility of 25 %.*

Recording a lower DM intake than was actually achieved would also have decreased digestibility. Deer did not have the opportunity to increase intake of the pelleted ration but they may have been able to increase DM intake through consumption of bedding material, wood fibres from pen walls or pelage.

Consumption of bedding material is possible but unlikely. Deer in Group 1 were placed on wire mesh false floors during the faecal collection stage and therefore had no access to the wood shavings. Even consumption of bedding immediately prior to faecal collection is unlikely because shavings became quickly soiled and would have presumably been unpalatable to deer. Deer in Group 2, while having access to bedding over the collection period, would have also encountered rapid soiling of bedding. While there is evidence that deer from both groups consumed wood from pen walls and their own pelage, the quantities are likely to have been in the order of 30 g DM/day or less. Much larger quantities (100 - 200 g DM/day) are required to have negated the decrease in digestibility as intake declined (Figure 6.6).

Having established the positive effect of intake on apparent DM digestibility is unlikely to have been an artefact from imperfect faecal collection technique or unaccounted intake, the work of Owens and Goetsch (1986) may provide an alternative explanation. These authors reported microbial efficiency was positively correlated with the dilution rate of culture medium. The positive correlation resulted

from the decrease in the relative cost of maintenance to microbes where dilution rate of the medium was high. Extrapolated to a rumen environment, this would suggest a higher passage rate of the liquid phase of rumen contents (a possible consequence of a greater DM intake) would facilitate a decrease in rumen residence time of microbes and lead to increased efficiency. However, although it has been hypothesised that fluid passage rates may increase with intake, others (Iason *et al.*, 1995) have failed to measure significant differences in fluid passage rate between seasonally induced differences in intake.

An alternative explanation for the positive relationships between intake and digestibility reported here may be an increase in non-rumen digestion such as caecal and large intestinal digestion. A shift to increased hind-gut digestion has been suggested where intake increased from winter to summer (Grovum and Williams, 1977).

It is possible also that the effect may have been an artefact of the highly processed pelleted diet. although Freudenberger *et. al.*, (1994) achieved a similar result with lucerne hay and chaff. There is a need in the future to establish the existence of such an effect on other feeds, especially fresh forages. Although recent work has focused on the digestion of fresh herbages such as chicory and perennial ryegrass by deer (Hoskin *et al.*, 1995; Kusmartono *et al.*, 1997), these have been at a single level of intake.

The findings from the present study require validation in further work but have important implications for energy budgets of weaner deer. Because of the size of the effect (an increase of 9 -15 percentage units as intake increases from ME_m to *ad lib.*) estimates of DDM intake based on DM intake are likely to lead to under feeding of restricted animals. Deer in a feed limited environment would not only be disadvantaged by a restricted DM intake but also by a reduced M/D as a result of the lower digestibility. Alternatively, an increase in feed availability not only increases DMI but increases MEI proportionately more through the intake effect on digestibility.

6.4 Conclusion

Deer in this study exhibited an intake-independent decrease in apparent *in vivo* DM digestibility of a pelleted feed from winter to spring by between 5 and 11 percentage units, presumably by increasing rumen fill and FOR. There was a positive relationship between intake and digestibility independent of season which could not be explained by potential errors in total faecal collection or unaccounted intake. This positive relationship between intake and digestibility is contrary to generally accepted principles, although the higher winter digestibility compared with spring at a common intake is consistent with current models.

It is not clear from these results whether the positive relationship between intake and digestibility is experimentally induced, or whether the same relationship holds for deer at pasture. Although this

effect has been shown in two different groups of animals in two different years, further work is needed to confirm this finding and begin to understand the mechanism behind the effect. However, if the positive relationship between digestibility and intake is a real effect, the consequences of limiting access of deer to feed are two fold. Not only will this restrict DM intake, but will limit DDM intake to a greater extent. The confirmation of this effect for deer at pasture has major implications for feed and energy budgets.

Chapter 7
General Discussion

The aim of the experiments reported in this thesis was to quantify any differences in liveweight gain of red and hybrid deer in a grazing environment and further to identify mechanisms which contribute to the greater rate of liveweight gain of hybrids compared with red deer. A comparison of genotypes was made in winter and spring which allowed for seasonal comparisons of the observations.

Genotype

Initially, a grazing study (stage I) was established to determine the liveweight gain response of both genotypes to pasture allocation. This study identified that there was little effect of pasture allowance on liveweight gain during winter but large effects in spring. The response in liveweight gain to increasing allowance was larger for hybrids compared with red deer in spring but not during winter and summer. This study was the first to report a pasture allowance - liveweight gain relationship for deer rotationally grazed in winter, spring and summer for two different genotypes. However, the utility of this information was limited by the specific pasture high - pasture allowance combinations used and the lack of replication. It was unclear from this study whether the genotype difference in liveweight gain was a result of different feed intake at a common pasture allowance or a result of possible differences in various components of energy metabolism.

The implication for producers from this first study is that during spring (mid August – December), a pasture allowance between 4 and 10 kg DM/h/day is desirable, depending on genotype and productivity targets. There is little advantage in increasing pasture allowance over 4 kg DM/h/day for red deer as it is likely *ad lib.* intake is achieved at this pasture allowance. Higher allowances are required for hybrid deer for them to achieve *ad lib.* intake and exhibit their greater potential for growth.

In a subsequent indoor experiment (Chapter 4a) deer were offered a pelleted concentrate diet *ad lib.* (as the largest difference between genotypes occurred at the highest pasture allowances in the previous experiment), to determine *ad lib.* intake and liveweight gain of each genotype. This study concluded that while the relative intake of red and hybrid deer was similar, both absolute and relative liveweight gain was greater for hybrids in spring compared with red deer. These results suggested a greater feed intake could not explain all the greater liveweight gain of hybrids compared with red deer so the study moved to more detailed energy balance experiments (stage IIa).

In the experiment reported in Chapter 4b, red and hybrid weaner stags were fed different quantities of a pelleted concentrate diet to estimate the ME requirement for maintenance. A higher (30%) ME requirement for zero liveweight gain was recorded for hybrid deer compared with red deer in both winter and spring. Literature values of ME_m differ between red deer and elk, but this study suggests that 25% elk genes in a hybrid is enough to elevate ME_m above that of red deer in an indoor environment.

In a further study involving 28 individually penned deer, liveweight gain, body weight gain and gain of adipose, lean and bone tissue (through CT scanning) were recorded. This study was an energy balance study involving repeated measurements on the same deer, rather than a subset of a common group of animals as in traditional comparative slaughter - type experiments. It also involved deer on a wide range of feeding levels during both winter and spring where previously only *ad lib.* and a single restricted intake had been used (for example Suttie and Hamilton, 1983).
There was a trend in this study, for red deer to deposit a greater amount of adipose in spring and less in winter than their hybrid counterparts although the difference did not reach significance.

Body composition data from this experiment provided input for an energy balance study (Chapter 5b). This showed that red and hybrid deer did not differ in their response in either energy retention or whole body weight gain to changes in ME intake in either winter or spring. This was despite differences in liveweight gain between genotypes.

If red deer deposited more adipose and less lean in weight gain (as suggested above) and therefore had a higher energy value of gain, then on this basis liveweight gain would be lower at the same ME intake (as observed) given similar k_f and k_p values. However, in neither winter (Figure 5.15) nor spring (Figure 5.16), was there a difference between genotypes in the energy value of gain and no difference in k_g. This suggests there should have been no difference in the energy required per unit liveweight gain between genotypes, yet at high intake, hybrids gained liveweight faster than red deer. Since there is little evidence for differences in the composition of gain body gain between genotypes, apparent changes in gut weight and gut content weight are likely to reconcile the differences between genotypes in liveweight gain. This illustrates a weakness of using liveweight gain as a measure of animal performance. However, further work is required to confirm such large changes in gut fill are real and that genotypes differ in gut fill across a range of allowances.

Season

The study of body composition changes showed significant seasonal differences in the relative growth of tissues with bone growing relatively faster and adipose relatively slower in winter compared with spring. There is evidence from previous work with sheep (Forbes *et al.* 1979; 1981) that long day length stimulates the growth of non-fat tissues at the expense of fat. This study also showed that on a restricted intake, simultaneous fat catabolism and lean tissue gain took place, especially in spring.

Although this study set out to identify and quantify differences between genotypes, seasonal differences were often more prominent than the genotype effect.

There were no seasonal differences in liveweight gain at a common intake in either of the indoor experiments reported (Chapter 4 and Chapter 5b). This may have been confounded by changes in the weight of gut and gut contents since the ME requirement for maintenance of whole body weight was greater in spring than winter and the energy cost of whole body weight gain was greater in winter than in spring. The implication of this is that while deer on restricted diets may increase whole body weight faster in winter than in spring, this may not be totally reflected in terms of liveweight gain.

In summary, this thesis has be able to show differences between red deer and hybrids and between seasons not previously reported. These are presented in general terms in Table 7.1.

Table 7.1 *Differences between red and hybrid deer based on data in this thesis.*

Difference between		Genotype	Season
Winter ad lib intake	(relative)	No difference	
	(absolute)	Greater for hybrids	
Spring *ad lib* intake	(relative)	Greater for hybrids	
	(absolute)	Greater for hybrids	
Max. winter liveweight gain		Possibly greater for red deer	
Max. spring liveweight gain		Greater for hybrids	
Ad lib. intake			Greater in spring
Max liveweight gain			Greater in spring
ME_m (liveweight)		Greater for hybrids in spring	No difference
ME_m (energy)		No difference	Greater in spring
Energy cost of liveweight gain (MJ/kg)		Reds maybe higher in spring	No difference
Energy cost of whole body gain (MJ/kg)		No difference	Greater in winter
Energy cost of energy gain		No difference	Greater for winter
k_p & k_f		No difference*	No difference*
Digestibility		No difference	Higher in winter

* no evidence of difference but based on limited data.

An attempt to apportion the genotype differences in liveweight gain in spring to measured differences in composition of gain and *ad lib* intake is made in Figure 7.1. Liveweight gain of red and hybrid deer was calculated using ME_m (Chapter 4), liveweight (Chapter 5), *ad lib.* intake (Chapter 4) and the cost of livewight gain (Chapter 4) for each genotype. The calculation is that used in Chapter 4. Results of this are outlined in Figure 7.1.

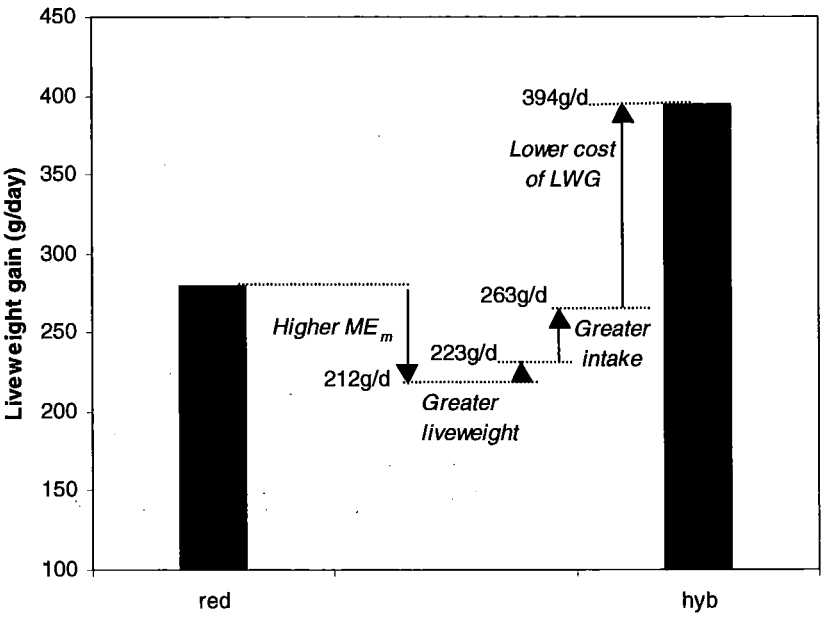


Figure 7.1 *The relative contribution of between - genotype differences in ME_m, liveweight, voluntary feed intake and energy cost of gain to the expected liveweight gain of hybrids relative to red deer.*

The difference between genotypes in liveweight gain was explained in this model by hybrids having a higher requirement for maintenance but a greater liveweight, a greater intake and a lower cost of liveweight gain compared with red deer. The lower cost of liveweight gain, although not significantly different, explained a large amount of the difference between genotypes. The predicted liveweight gain of red deer (290 g/day) and hybrids (394 g/day) was comparable to those observed in Chapter 5b (see Table 5.10) of 340 g/day and 438 g/day for red and hybrid deer, respectively. The differences between genotypes in winter were small and consequently a similar model has not been presented for the winter period.

The discrepancy between liveweight gain and whole body weight gain (possibly caused by apparent changes in gut fill) is a limitation to the interpretation of this work and leads to two different models of weight gain in young deer. The same model as used for liveweight gain above was applied for whole body weight gain (Figure 7.2). Because there was no difference between genotypes in maintenance requirement for zero whole body weight gain or in the energy cost of whole body weight gain, genotype differences were explained in this model by differences in liveweight and intake only.

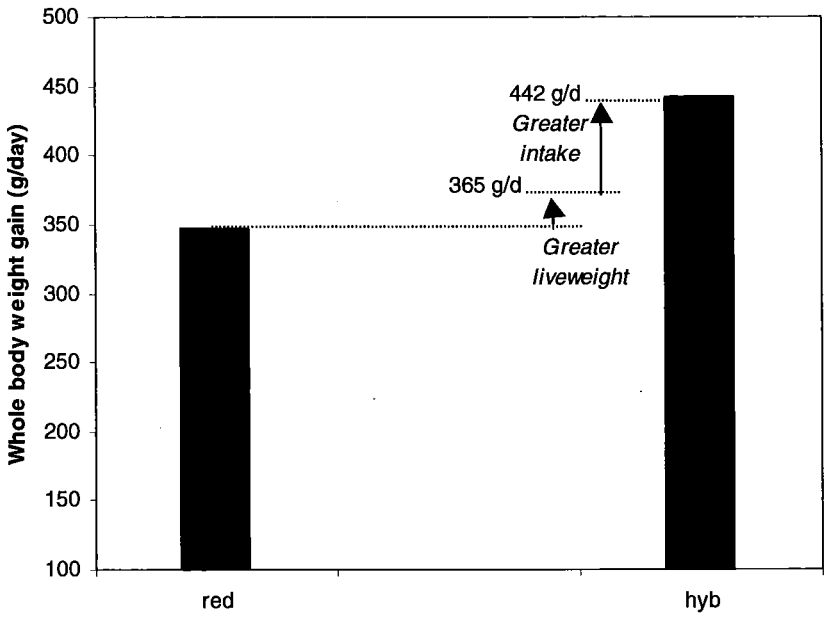


Figure 7.2 *The relative contribution of between - genotype differences in liveweight and voluntary feed intake to the expected whole body weight gain of hybrids relative to red deer.*

The model was also used to illustrate seasonal differences in whole body weight gain when genotypes were combined (Figure 7.3).

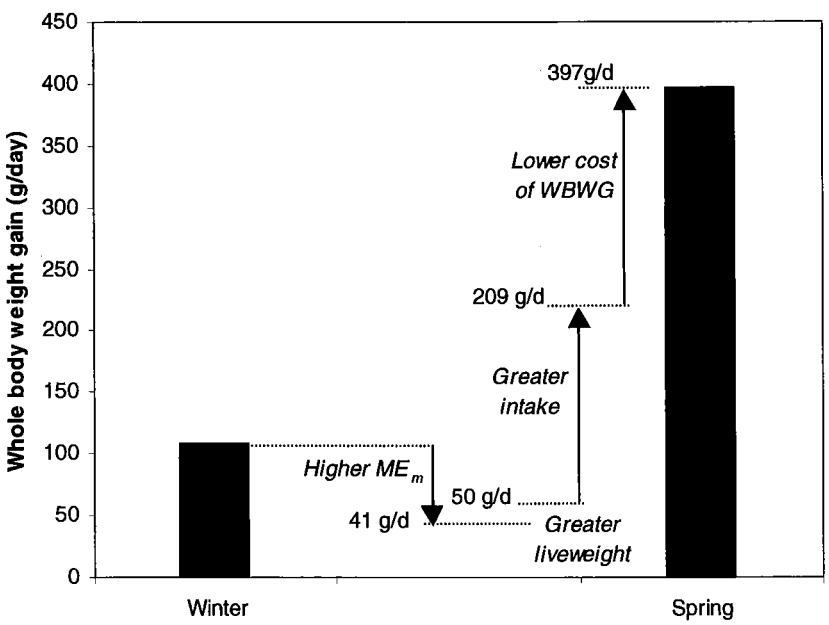


Figure 7.3 *The relative contribution of between - season differences in ME_m, liveweight, voluntary feed intake and energy cost of gain to the expected whole body weight gain in spring relative to winter.*

Relative to winter, deer gained whole body weight faster in spring due to a greater intake and a lower cost of whole body weight gain as a result of a leaner composition of whole body weight gain.

Low winter liveweight gain of weaners has been regarded as a limitation in early venison production. Winter liveweight gain on pasture is typically between 50 and 100 g/day and significantly increasing this would advance slaughter date. Results from this thesis suggest that while winter liveweight gain of 200 g/day may theoretically be possible (depending on liveweight and ME of the diet) they require much higher intake than would be required for the same liveweight gain in spring. For example a 60 kg red deer gaining liveweight at 50 g/day would consume about 900 g DM/day. Increasing winter liveweight gain to 150 g/day for the same animal would require an additional 425g DM/day. However, this extra DM intake consumed in the spring (by a 60 kg red deer) would increase liveweight gain from 50 g/day to about 210 g/day.

It is recommended in light of findings from this research that during winter (June – mid August) weaners be restricted to small pasture allowances. In addition to the natural seasonal depression in intake, liveweight gain for both genotypes is limited during winter by the tendency to increase the energy value of the gain and consequently reduce liveweight gain per unit intake. On the other hand, low liveweight gain may result in undesirable fat loss. To maintain a positive energy balance in winter, either genotype needed to increase liveweight at a rate of 40 g/day. The 50-100 g/day as previously proposed (Fennessy and Milligan, 1987) appears to be an appropriate compromise between zero energy balance and the low utilisation of pastures necessary to achieve high intakes. Given the rapid loss of fat in early spring recorded in this experiment, body condition of weaners at this time (which inevitably reflects winter nutrition) may have a significant effect on early spring growth. This hypothesis requires further investigation.

Differences exist between red deer and hybrids in intake and liveweight gain and these have implications for producers. However, there are much larger seasonal and probably maturity-related differences in energy cost of gain, energy required for maintenance and relative growth of adipose, lean and bone tissue exhibited by both genotypes. These differences can be exploited in deer production systems.

Table A1.1. *Correlation (Pearson's correlation coefficient) between all variables during winter. Figures in bold represent a significant correlation. Description of terms is presented on page 144.*

	Allow															
1/All	**-0.970**	1/All														
Per-H	**0.990**	**-0.951**	Per-H													
1/P-H	**-0.946**	**0.989**	**-0.943**	1/P-H												
Geno	0.000	0.000	0.000	0.000	Geno											
Par	**0.256**	**-0.255**	**0.256**	**-0.255**	**0.709**	Par										
Sou	0.092	-0.117	0.079	-0.112	-0.044	-0.064	Sou									
LWG	0.034	-0.041	0.069	-0.079	0.030	-0.057	0.149	LWG								
$LWG^{0.75}$	0.032	-0.039	0.065	-0.076	-0.043	-0.107	0.153	**0.993**	$LWG^{0.75}$							
Lwt	**0.225**	**-0.220**	0.209	-0.201	**0.759**	**0.629**	0.050	**-0.198**	**-0.288**	Lwt						
PreH	**0.958**	**-0.992**	**0.951**	**-0.996**	0.018	**0.268**	0.108	0.065	0.062	0.215	PreH					
1/PreH	**-0.818**	**0.923**	**-0.815**	**0.959**	-0.020	**-0.240**	-0.119	-0.105	-0.100	-0.178	**-0.945**	1/PreH				
PostH	**0.971**	**-0.909**	**0.989**	**-0.903**	0.061	**0.301**	0.061	0.068	0.061	**0.242**	**0.919**	**-0.761**	PostH			
PreM	**0.892**	**-0.942**	**0.911**	**-0.979**	0.042	**0.276**	0.095	0.123	0.116	**0.196**	**0.974**	**-0.966**	**0.886**	PreM		
1/PreM	**-0.785**	**0.889**	**-0.796**	**0.941**	-0.047	**-0.251**	-0.108	-0.134	-0.127	-0.178	**-0.925**	**0.993**	**-0.750**	**-0.970**	1/PreM	
PostM	**0.991**	**-0.982**	**0.988**	**-0.973**	0.004	**0.265**	0.086	0.051	0.048	**0.219**	**0.982**	**-0.874**	**0.966**	**0.938**	**-0.850**	PostM
Avail.	**0.998**	**-0.968**	**0.995**	**-0.950**	0.011	**0.265**	0.088	0.046	0.043	**0.224**	**0.963**	**-0.827**	**0.981**	**0.909**	**-0.800**	**0.994**

Table A1.2. *Correlation (Pearson's correlation coefficient) between all variables during spring. Figures in bold represent a significant correlation. Description of terms is presented on page 144.*

	LWG															
$LWG^{0.75}$	**0.983**	$LWG^{0.75}$														
All	**0.473**	**0.471**	All													
1/A	**-0.587**	**-0.596**	**-0.915**	1/A												
P-H	**0.534**	**0.536**	**0.983**	**-0.969**	P-H											
1/p-h	**-0.604**	**-0.619**	**-0.800**	**0.973**	**-0.888**	1/p-h										
Geno	**0.361**	**0.256**	0.000	0.000	0.000	0.000	Geno									
Par	**0.228**	0.158	-0.153	0.179	-0.168	0.179	**0.657**	Par								
Sou	0.054	0.029	0.045	-0.062	0.056	-0.065	0.019	0.026	Sou							
Lwt	**0.509**	**0.379**	0.194	**-0.266**	**0.227**	**-0.288**	**0.727**	**0.492**	0.124	Lwt						
PreH	**0.610**	**0.618**	**0.830**	**-0.983**	**0.914**	**-0.994**	0.034	-0.161	0.072	**0.304**	PreH					
1/PH	**-0.583**	**-0.601**	**-0.670**	**0.907**	**-0.777**	**0.978**	-0.006	0.170	-0.066	**-0.298**	**-0.956**	1/PH				
PostH	**0.570**	**0.572**	**0.909**	**-0.989**	**0.967**	**-0.956**	0.011	-0.184	0.074	**0.258**	**0.979**	**-0.882**	PostH			
PreM	**0.602**	**0.615**	**0.777**	**-0.965**	**0.873**	**-0.998**	**0.014**	-0.172	0.074	**0.298**	**0.995**	**-0.980**	**0.954**	PreM		
1/PM	**-0.576**	**-0.594**	**-0.672**	**0.909**	**-0.780**	**0.979**	0.005	0.180	-0.069	**-0.289**	**-0.958**	**1.000**	**-0.885**	**-0.981**	1/PM	
PostM	**0.564**	**0.567**	**0.918**	**-0.983**	**0.973**	**-0.940**	-0.003	-0.189	0.074	**0.243**	**0.967**	**-0.854**	**0.997**	**0.938**	**-0.859**	PostM
Avail	**0.500**	**0.497**	**0.997**	**-0.938**	**0.993**	**-0.835**	0.012	-0.152	0.050	**0.215**	**0.866**	**-0.712**	**0.936**	**0.816**	**-0.714**	**0.943**
GPM	**0.602**	**0.613**	**0.763**	**-0.950**	**0.867**	**-0.977**	0.013	-0.173	0.081	**0.287**	**0.987**	**-0.946**	**0.957**	**0.986**	**-0.949**	**0.950**
Grass	-0.172	-0.181	**-0.441**	**0.420**	**-0.390**	**0.414**	0.000	0.059	0.020	-0.128	**-0.355**	**0.446**	**-0.322**	**-0.369**	**0.438**	**-0.275**
Clover	-0.008	-0.001	0.197	-0.133	0.118	-0.128	-0.000	-0.006	-0.042	0.049	0.062	-0.178	0.031	0.081	-0.169	-0.017
Dead	**-0.353**	**-0.367**	**-0.624**	**0.678**	**-0.618**	**0.688**	-0.000	0.112	-0.008	**-0.207**	**-0.637**	**0.710**	**-0.593**	**-0.652**	**0.704**	**-0.548**
Stem	**-0.455**	**-0.483**	**-0.209**	**0.579**	**-0.362**	**0.750**	0.000	0.125	-0.052	**-0.258**	**-0.699**	**0.866**	**-0.546**	**-0.766**	**0.863**	**-0.505**
Repro	**0.345**	**0.364**	**0.474**	**-0.609**	**0.498**	**-0.670**	-0.000	-0.105	0.009	**0.216**	**0.605**	**-0.737**	**0.520**	**0.642**	**-0.730**	**0.466**

	Avail					
GPM	**0.806**	GPM				
Grass	**-0.420**	**-0.216**	Grass			
Clover	0.164	-0.080	**0.955**	Clover		
Dead	**-0.621**	**-0.522**	**0.945**	**-0.808**	Dead	
Stem	**-0.265**	**-0.731**	**0.288**	-0.100	**0.514**	Stem
Repro	**0.482**	**0.508**	**-0.914**	**0.789**	**-0.974**	**-0.650**

Table A1.3. *Correlation (Pearson's correlation coefficient) between all variables during summer. Figures in bold represent a significant correlation. Description of terms is presented on page144.*

	LWG															
$LWG^{0.75}$	**0.941**	$LWG^{0.75}$														
All	**0.543**	**0.545**	All													
1/A	**-0.589**	**-0.616**	**-0.947**	1/A												
P-H	**0.580**	**0.554**	**0.984**	**-0.943**	P-H											
1/p-h	**-0.608**	**-0.612**	**-0.896**	**0.983**	**-0.917**	1/p-h										
Geno	0.104	-0.154	0.000	0.000	0.150	-0.134	Geno									
Par	0.067	-0.099	0.060	-0.079	0.175	-0.180	**0.680**	Par								
Lwt	0.164	-0.061	0.202	**-0.246**	**0.310**	**-0.342**	**0.684**	**0.593**	Lwt							
PreH	**0.575**	**0.616**	**0.872**	**-0.982**	**0.877**	**-0.987**	0.006	0.090	**0.260**	PreH						
1/PH	**-0.605**	**-0.658**	**-0.736**	**0.911**	**-0.750**	**0.942**	0.004	-0.105	**-0.264**	**-0.963**	1/PH					
PostH	**0.539**	**0.564**	**0.951**	**-0.991**	**0.950**	**-0.970**	0.020	0.077	**0.249**	**0.971**	**-0.873**	PostH				
PreM	**0.505**	**0.555**	**0.822**	**-0.953**	**0.828**	**-0.962**	0.007	0.073	**0.253**	**0.988**	**-0.948**	**0.956**	PreM			
1/PM	**-0.541**	**-0.592**	**-0.801**	**0.949**	**-0.808**	**0.965**	-0.000	-0.079	**-0.259**	**-0.990**	**0.976**	**-0.938**	**-0.994**	1/PM		
PostM	**0.420**	**0.458**	**0.876**	**-0.940**	**0.875**	**-0.923**	0.019	0.048	**0.233**	**0.942**	**-0.834**	**0.972**	**0.963**	**-0.932**	PostM	
Avail	**0.550**	**0.561**	**0.995**	**-0.973**	**0.982**	**-0.931**	0.003	0.065	0.217	**0.915**	**-0.792**	**0.977**	**0.874**	**-0.855**	**0.914**	Avail
GPM	**0.385**	**0.456**	**0.574**	**-0.792**	**0.592**	**-0.835**	0.013	0.069	**0.240**	**0.887**	**-0.908**	**0.796**	**0.938**	**-0.940**	**0.858**	**0.652**
Grass	**-0.713**	**-0.726**	**-0.832**	**0.895**	**-0.835**	**0.898**	0.000	-0.129	**-0.246**	**-0.875**	**0.888**	**-0.832**	**-0.793**	**0.830**	**-0.694**	**-0.846**
Clover	**-0.474**	**-0.511**	**-0.908**	**0.970**	**-0.903**	**0.951**	-0.000	-0.047	**-0.231**	**-0.967**	**0.868**	**-0.990**	**-0.973**	**0.950**	**-0.994**	**-0.943**
Dead	**0.374**	**0.447**	**0.559**	**-0.781**	**0.576**	**-0.823**	0.000	0.052	**0.233**	**0.878**	**-0.901**	**0.785**	**0.931**	**-0.934**	**0.851**	**0.638**
Stem	**-0.545**	**-0.606**	**-0.607**	**0.829**	**-0.627**	**0.878**	0.000	-0.100	**-0.261**	**-0.913**	**0.983**	**-0.791**	**-0.917**	**0.950**	**-0.779**	**-0.676**
Repro	**0.486**	**0.536**	**0.835**	**-0.954**	**0.838**	**-0.957**	0.000	0.059	**0.246**	**0.983**	**-0.929**	**0.963**	**0.998**	**-0.988**	**0.977**	**0.885**

GPM	GPM				
Grass	**-0.622**	Grass			
Clover	**-0.850**	**0.764**	Clover		
Dead	**0.999**	**-0.607**	**-0.842**	Dead	
Stem	**-0.942**	**0.803**	**0.805**	**-0.939**	Stem
Repro	**0.928**	**-0.774**	**-0.983**	**0.922**	**-0.895**

Key

Allowance	allowance on a metabolic liveweight basis
1/All =	reciprocal of allowance on a metabolic liveweight basis
Per-H =	allowance on a per head basis
1/per - head =	reciprocal of allowance on a per head basis
Geno =	genotype, red or hybrid
Sou =	original source of animals
Avail =	Availability (pre-grazing height x allowance per head)
Par =	genotype determined by blood typing (expressed as the proportion of elk genes)
LWG =	liveweight gain (g/day)
LWG $^{0.75}$	liveweight gain (g/W $^{0.75}$/day)
Liveweight =	initial liveweight (kg) for each
PreH =	pre-grazing pasture height
1/PreH =	reciprocal of pre grazing pasture height
Post H =	post-grazing pasture height
PreM =	pre-grazing pasture mass
1/PreM =	reciprocal of pre-grazing pasture mass
PostM =	post-grazing pasture mass
GPM =	green pasture mass (pre-grazing pasture mass x (1-(dead material + reproductive growth %))
Grass =	percentage of grass leaf in the sward
Clover =	percentage of clover in the sward
Dead =	percentage of dead material in the sward
Stem =	percentage of pseudo-stem in pasture
Repro =	percentage of reproductive growth

Appendix II

Average LWG (g/day) (1 March to 1 Nov)

March liveweight (kg)	percentage of animals reaching 92 kg					
	100	125	150	175	200	225
40	0	0	0	1	9	44
45	0	0	0	7	38	82
50	0	0	5	33	78	98
55	0	4	28	73	97	100
60	3	23	68	95	100	100
65	19	63	94	100	100	100
70	57	92	100	100	100	100

Figure A2.1 *The percentage of deer in a group reaching 92 kg liveweight by 1 November based on a range of March weaning weights and rates of liveweight gain. Stippled and shaded areas represent likely scenarios for red and hybrid deer, respectively.*

Average LWG (g/day) (1 March to 1 Oct)

March liveweight (kg)	percentage of animals reaching 92 kg					
	100	125	150	175	200	225
40	0	0	0	0	0	5
45	0	0	0	0	5	29
50	0	0	0	6	29	69
55	0	0	6	30	70	94
60	0	6	30	70	94	100
65	6	31	71	94	100	100
70	31	71	95	100	100	100

Figure A2.2 *The percentage of deer in a group reaching 92 kg liveweight by 1 October based on a range of March weaning weights and rates of liveweight gain. Stippled and shaded area represents likely scenarios for red and hybrid deer respectively.*

Appendix III

Table A3.1. Weekly mean daily intake (g DM/hd/day) of group-fed deer in winter and spring for deer in Chapter 4b.

	Week	1	2	3	4	5	6	7	8	9	Mean
Winter	**Red**	1469	1703	1398	1626	1677	1667	1797	1681		1627
	Hyb	1679	1715	1390	1705	1912	1772	1885	1878		1742
Spring	**Red**	2554	2080	2023	2533	2642	2550	2567	2486	2434	2415
	Hyb	2736	2185	2125	2728	2884	2886	2745	3018	2910	2653

Appendix IV

Establishing appropriate grey scale ranges for image analysis.

A4.0 Introduction

Prior to the analysis of CT images, the electronic *dissection* software (*Autocat*, N.Jopson, *pers com*) was calibrated to ensure correct identification of adipose, lean and bone tissue in CT images.

In previous studies using this equipment, (Nsoso, 1995) calibration of dissection software has been achieved by identifying areas in an image which contain exclusively adipose, lean or bone tissue. The adipose sample areas for example, were then submitted to A*utocat* and the grey scale range for adipose tissue adjusted so that all pixels in adipose-only-images were recognised as adipose tissue. The same calibration was applied for lean and bone.

However, as outlined in this appendix, although areas of homogenous tissue do have discrete grey scale distributions, analysis of whole images revealed overlapping adipose and lean tissue grey scale distributions, raising concerns about the appropriate grey scale truncation point, especially between adipose and lean tissue. In addition, previous calibrations have been for sheep images rather than deer and therefore image analysis software required re-calibration.

A4.1 Materials and Methods

A4.1.1 Analysis of grey scale distribution

Images from an *ad lib.* fed animal were used in the calibration of *Autocat* as they were the only images that contained significant areas of adipose tissue. (Figure A4.4). *Photomagic* (Micrografx Inc) was used to "dissect out" areas of adipose, lean and bone from sites in the shoulder, thorax and rump. These were repeatedly submitted to *Autocat* increasing the grey scale range "dissected" by 5 grey scale value ranges with each submission to form a grey scale distribution of pixels. A distribution of grey scales was also generated for the three entire images.

A4.1.2 Spatial distribution

The spatial distribution of pixels in various ranges of grey scale was studied using *Catwoman* software (N.Jopson, pers com.). *Catwoman* highlighted pixels in a specified grey scale range. Only the rump area which contained significant areas of adipose lean and bone were used in this study.

A4.2 Results & discussion

The total area (mm^2) of tissue in each grey scale of dissected adipose lean and bone from 3 separate sites (shoulder, thorax and rump) is given in Figure A4.1. The distributions of both adipose and lean

appear to be normally distributed and discrete. The mean (± SD) grey scale for adipose, lean and bone was 87.1 ± 5.2, 169 ± 5.7 and 254 ± 0.0 respectively. The wide range in density of bone was collapsed into a singe grey scale (254) by *Bitman* (N.Jopson, pers com.). There was no difference in either the mean or standard deviation of distributions between red deer and hybrids.

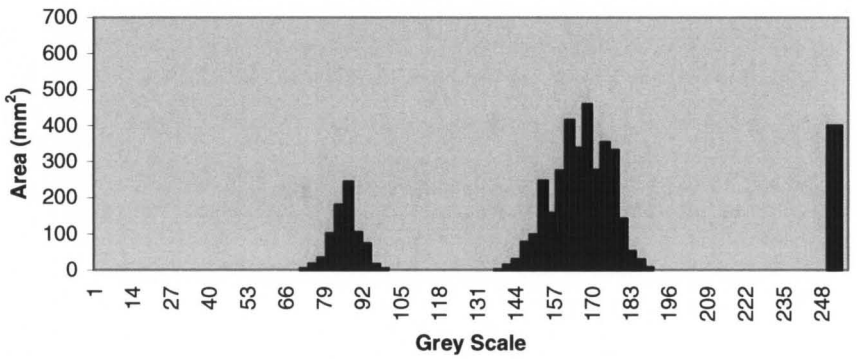


Figure A4.1. *The grey scale distribution of homogenous areas of adipose lean and bone from the rump of a ad. lib. fed red deer and the dissection range employed by Nsoso (1995).*

Based on the grey scale distribution of homogeneous tissue the *Autocat* range employed by Nsoso, (1995) (1-130, 131-250 and 251-255 for adipose, lean and bone, respectively) would have correctly identified all tissues in this example. They also met Nsoso's (1995) criteria that the range between grey scale truncation points be greater than 3 times the standard deviation from the mean for each distribution.

However when the grey scale distribution of a whole animal image was generated the individual tissue distributions were much less discrete (Figure A4.2).

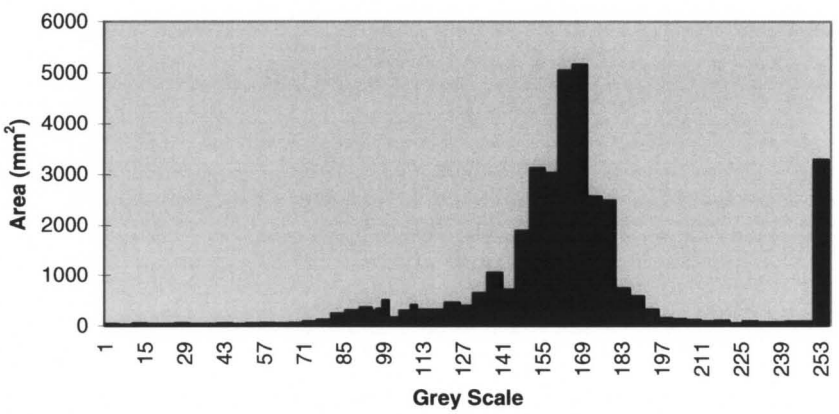


Figure A4.2 *Grey scale distribution of 3 images (shoulder, thorax and rump) of a deer in good condition*

While it is evident that the three distributions seen in Figure A4.1 still exist, there is area in the whole image which occurs outside the grey scales of homogenous tissue. Identifying what these *extra* pixels

represented was considered necessary before a decision to include or exclude these from analysis or include as adipose or lean was made. To aid in identification the spatial distribution of the extra pixels within an image was generated using *Catwoman* software.

Figure A4.3 shows the spatial distribution of pixels in the grey scale range 1-70, a grey scale range not containing pixels in homogeneous tissue. The pixels in this range largely occurred around the outside of the image, were a small percentage (2%) of the total number of pixels and probably occurred due to a partial voluming effect. This occurred when more than one tissue was found in a single pixel, such as the skin air interface. The grey scale assigned to that pixel would have reflected the average density of each tissue and the relative amounts of each tissue within the pixel. Pixels which contained mostly air (grey scale 0) but a little adipose (grey scale about100) had an average grey scale close to 0 simply because of the greater proportion of air in the pixel. Air-tissue pixels with increasing amounts of tissue would have an increasingly greater grey scale value.

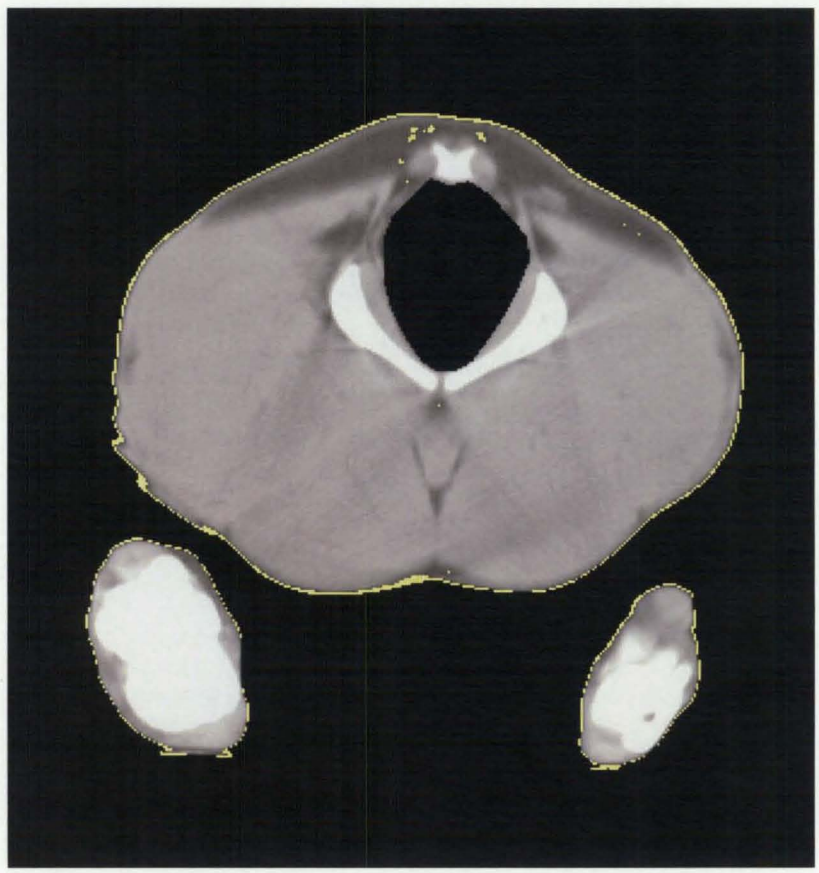


Figure A4.3. *A rump CT image showing the distribution of pixels corresponding to a grey scale between 1-70 for a well conditioned deer. Highlighted pixels represent 2% of total pixels and probably represent a partial voluming effect.*

Consequently, those pixels which contain greater than half their area as air should be left out. The tissue area lost by this action would be compensated for by the air included in those pixels with greater than half their area as tissue.

It is likely that the partial voluming effect takes place between the air and skin. Because the image is placed at a random position within the pixel matrix a random distribution of pixel air tissue ratios is expected and hence similar numbers of pixels in each greyscale. Assuming that pixels containing 100% skin tissue rarely have a grey scale value of less than 70 (Figure A4.1) on average all pixels with a grey scale value of greater than 35 should contain more than half their area of tissue. The lower value therefore for adipose should be 35.

Although adipose and lean distributions do not appear to overlap (FigureA4.1), partial voluming at the adipose-lean interface creates pixels with a grey scale value in this range. Applying the same rationale for the adipose-lean interface as for skin-air interface a grey scale value of less than 120 (intermediate of the upper adipose value 100 and the lower lean value 140 from Figure A4.1) will contain more adipose than lean and therefore should be considered as a adipose pixel while those greater than 120 will contain more lean than adipose and therefore should be considered as lean. Therefore pixel in a grey scale between 35 and 120 (Figure A4.1) were considered to represent adipose tissue.

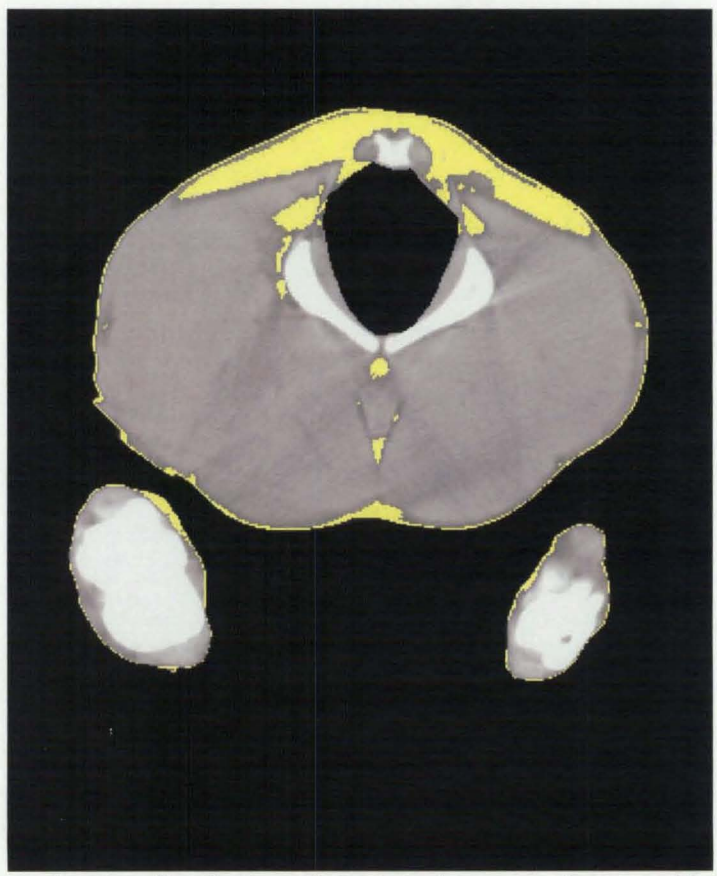


Figure A4.4 *CT Image showing distribution of pixels in the greyscale range 35-120 corresponding with adipose. Highlighted pixels are 11% of total pixels*

The truncation point between lean and bone was determined in similar fashion. Lean had an upper range of 190 grey scale (Figure A4.1) and the mid-point between lean and bone (grey scale 256) was 223, which was adopted as the truncation point between lean and bone. Therefore, lean was defined by pixels with a grey scale between 121 and 223 (Figure A3.5) and bone between 224 and 256 (Figure A4.6).

The number of images on which this calibration was based is small (n = 3) and a larger sample size may have revealed a slightly different distribution. In light of this, a sensitivity analysis was undertaken to demonstrate how sensitive the final analysis was to small changes in grey scale truncation values.

Table A4.1. *Total weight (g) and percentage of whole animal of dissected adipose and lean tissue at various grey scale ranges.*

Adipose			Lean		
Grey scale	Wt (g)	% of animal	Grey scale	Wt (g)	% of animal
1-120	3922	8.7	120-223	35322	80.2
1-130	5313	11.8	130-223	33931	77.0
35-120	3513	7.9	130-233	34165	77.1
40-120	3458	7.4			
40-125	4180	9.4			

Excluding pixels with more than half their area as air had little effect (1%) on total adipose dissected (1-120 vs 35-120). A 5 grey scale shift in the lower value 40-35 realised a 0.2% change in total adipose dissected. However, extending the upper grey scale range for adipose from 120 to 125 increased total dissectible adipose by 1.7%. Similarly, for lean, reducing the lower grey scale value by 10 from 130 to 120 increased total dissectible lean by 2.2 % or 1.39 kg. Increasing the upper value by the same amount had little effect (0.1%) on total dissectible lean.

The mass of tissue was relatively insensitive to the lower adipose and upper lean grey scale settings because of the low frequency of pixels in these areas (Figure A4.6). However, the truncation point between adipose and lean has a relatively large effect on both tissues.

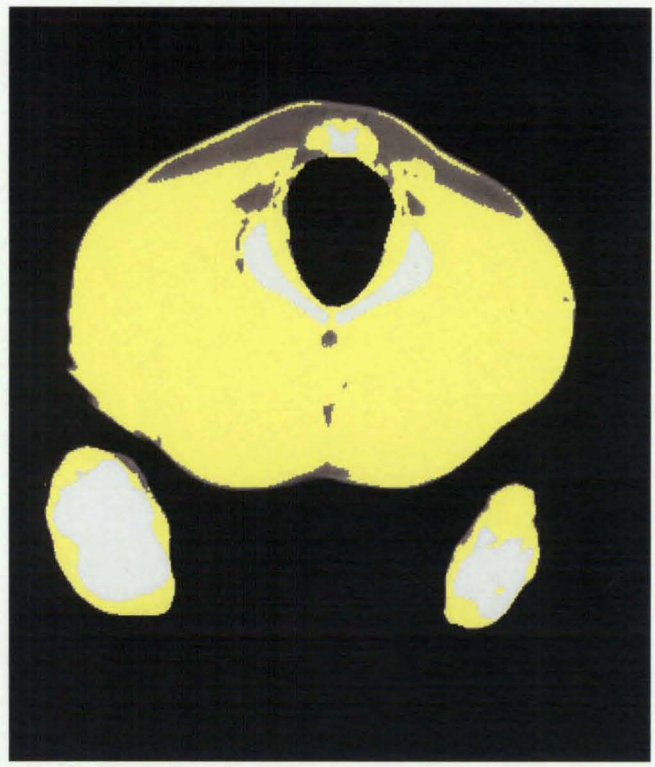


Figure A4.5 *CT image with pixels in the lean (121-223) grey scale range. About 75 % of total image pixels are highlighted*

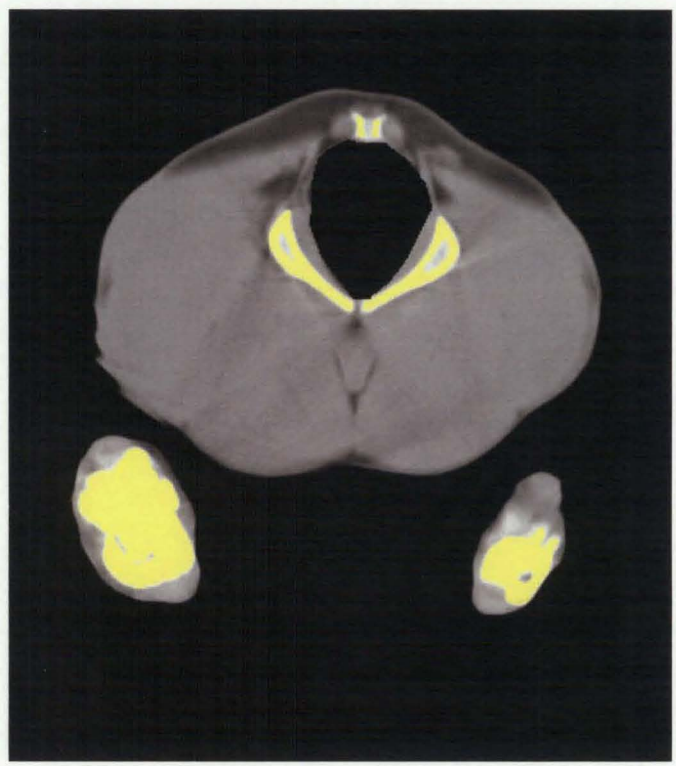


Figure A4.6. *CT image of pixels at 255 grey scale corresponding to bone. A total of 11% of pixels are highlighted.*

A4.3 Conclusion

When whole images were analysed there were no discrete distributions for adipose and lean, rather a continuum of grey scales as a result of partial voluming where two different tissues (or air) were present in a single pixel. The truncation points within the grey scale range which determined adipose lean and bone were determined such that it was the most abundant tissue in each pixel which decided to which tissue group it was associated. A sensitivity analysis indicated the final analysis of the proportions of adipose lean and bone present in each set of images was generally insensitive to small changes in truncation points.

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